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**Toward the Phylogeny of a
Fossil Species Flock:
Semionotid Fishes from a
Lake Deposit in the
Early Jurassic Towaco Formation,
Newark Basin**

Amy Reed McCune

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**Peabody Museum
of Natural History
Yale University**

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TOWARD THE PHYLOGENY OF A FOSSIL
SPECIES FLOCK: SEMIONOTID FISHES FROM
A LAKE DEPOSIT IN THE EARLY JURASSIC
TOWACO FORMATION, NEWARK BASIN

AMY REED McCUNE

ABSTRACT

A radiation of fishes in the family Semionotidae is preserved in the sedimentary record of the great rift lakes that existed during the Late Triassic and Early Jurassic in eastern North America (Newark Supergroup). Although species flocks—diverse groups of closely related species from geographically confined areas—have been described for several groups of living fishes, the Newark semionotids described herein are the first fossil, and the first non-teleost, species flock of fishes known.

The Newark lacustrine sedimentary record, which has preserved complete articulated semionotids, is itself exceptional. Within each of the several lake basins, sediments represent a repeating sequence through time of forming and evaporating lakes. For nearly one-third of each individual lake episode of the many preserved within a given basin, the sediments are varved, thereby providing a yearly chronology for eventual study of the pattern of diversification of semionotids.

Nearly 2,000 specimens were collected with precise microstratigraphic data from a single lake episode or sedimentary cycle in the Early Jurassic Towaco Formation of the Newark Basin, New Jersey. Based on this sample, 19 species are described. These species constitute only a small fraction of species known (but undescribed) from Newark lake deposits. Fifty-one meristic, morphometric, and qualitative characters are examined. Body shape and the morphology of the dorsal ridge scales are the most variable characters. Body shape is analyzed geometrically and by multivariate analysis of morphometric data. The morphology of the dorsal ridge scale series is characterized qualitatively. Following a discussion of character analysis, a tentative cladogram is presented for these and closely related European semionotids.

KEYWORDS

Semionotidae, adaptive radiation, rift lake deposits, Early Jurassic, Newark Supergroup, systematics, morphometrics.

1. INTRODUCTION

In a paper on the geology and mineralogy of Massachusetts, Edward Hitchcock (1819, p. 110) noted that impressions of fish could be found at the foot of Mt. Toby in the Connecticut River bed near Sunderland, Massachusetts. This passing remark by Hitchcock was the first published report of a semionotid fish from eastern North America. Although Hitchcock (1823) published figures of several of these semionotids, Louis Agassiz (1835) was the first to describe a Newark semionotid, naming it *Eurynotes tenuiceps*.

Following Hitchcock's discovery of semionotids at Sunderland, several paleontologists, including Loper (1893, 1899), W. C. Redfield (1839, 1841, 1843), J. H. Redfield (1837), Silliman (1821), and Gratacap (1886) discovered similar fish localities in Connecticut, New Jersey, and Massachusetts, in lake sediments now included in the Newark Supergroup (Olsen 1978). Early workers, recognizing the abundance and diversity of semionotids in Newark lake deposits, described numerous species (e.g., Newberry 1888). Unfortunately, most of these early descriptions are too vague to identify specimens, other than those originally figured, leading most twentieth-century workers to believe that more Newark semionotids have been named than actually exist (e.g., Schaeffer 1967).

The distinction between the closely related genera *Semionotus* Agassiz, to which most American species are referred, and *Lepidotes* Agassiz has been clouded by nomenclatorial problems, entangled in Agassiz's advocacy of the threefold parallelism (see McCune 1982, 1986; McCune and others 1984), and handicapped by the poor preservation of the few available specimens. This nomenclatorial confusion, combined with the overwhelming diversity of semionotids, probably discouraged scientific interest in Newark semionotids after the publication of Newberry's monograph in 1888.

In recent years, advances in our understanding of the lake environments (see Olsen 1980b) in which these Newark semionotids lived have revived motivation to work out the species-level systematics of semionotid fishes. We now know that many Newark lakes were large, deep, and perennially stratified. Although the lakes were very large and deep, on a geological time scale they were ephemeral. Induced by regular changes in climate, individual lakes formed, deepened, shallowed, and finally evaporated, roughly every 21,000–23,500 years (Van Houten 1969; Olsen 1980b, 1984a). Within the sedimentary record of individual lake histories, corresponding to the period of maximum lake transgression, abundant, whole, articulated fishes are preserved in sediments showing annual bedding structures (Van Houten 1969; Olsen 1980b).

Knowledge of these special paleontological and sedimentological circumstances has created new potential for understanding the evolution of diverse complexes of fishes in relation to the history of their lake environment. We have begun to outline the broad historical picture of the evolution of semionotids (McCune and others 1984), but many questions remain. How did the geological ephemerality of these great deep rift lakes in the Newark system affect colonization, migration, and evolution of semionotid fishes? If the regular climatic change that so profoundly influenced the levels of these lakes is general throughout the Phanerozoic, how does this climatic change affect modern lakes and the fishes living in them (see McCune and others 1984)? Can patterns of morphological change and diversification be calibrated to the year-by-year chronology preserved in the varved sequences within individual lake histories? Discussion of these questions relies heavily on species-level taxonomy as a basic vocabulary.

The overall goal of this ongoing research, then, is to take advantage of the

remarkable circumstances of the Newark fossil record and begin to develop a data base for future study of the pattern of diversification of semionotids through time. The broad paleontological and evolutionary scope of this research requires that 1) new collections of semionotids be made for individual lake records while paying careful attention to microstratigraphic detail, 2) an alpha taxonomy comparable to that for living fishes be developed for these and previously collected semionotids, 3) the relationships of these species be analyzed phylogenetically, and 4) the patterns of species distribution through time and space be mapped. The present work is a progress report for the semionotids collected from a single lake history, sedimentary cycle P4 in the Towaco Formation of the Newark Basin. Excavation of this particular lake cycle, which is the middle lake record in a succession of three temporally distinct lakes containing semionotids, allows for the future possibility of tracking semionotid faunas across two interlacustrine periods. The focus here is taxonomic; the microstratigraphic distribution of the species described here will be treated in a subsequent work.

The species-level taxonomy of semionotid fishes should be most useful for evolutionary and paleoecological investigations if these fossil species reflect biological species. Comparability of living and fossil species of fishes has previously been achieved to some degree (Schaeffer 1948, 1952; Schaeffer and Dunkle 1950; Schaeffer and others 1975; Schaeffer and McDonald 1978; Gaudant 1978; Grande 1982a, b), but one may suspect that a fossil species is often comparable to a living genus. Taking into account that it is an operational necessity to use a morphological species concept rather than the biological species concept for fossils and recognizing that certain characters will always be lacking, every attempt has been made to interpret variation in these fossils as one would if they were living fishes. I cannot assert that the species described here were at one time good biological species; at the very least, my attempt to categorize the variability in semionotids communicates the diversity of semionotid morphology. Instead, I view these species descriptions as hypotheses of biological species as inferred from available morphology. Reassuringly, however, initial results of studies on growth of two species of semionotids seem to show that, like different species of *Lepisosteus*, even closely related species of semionotids exhibit distinct patterns of scale growth (Thomson and McCune 1984).

The fish beds included in cycle P4 of the Towaco Formation were discovered at "Ryerson's Quarry" by W. C. Redfield. Redfield (1843) reported that at least three previously described species of semionotids were present at Pompton. He referred the fishes from Pompton to "*Paleoniscus fultus*" Agassiz (1833), "*Paleoniscus latus*" Redfield (1837), and "*Paleoniscus agassizii*" Redfield (1841) (all of which were later included in *Semionotus* by Woodward in 1895). Both *S. fultus* and *S. agassizii* are based on specimens from Boonton, New Jersey, that belong to the *S. elegans* group (sensu Olsen and others 1982). *Semionotus latus*, based on a specimen from the Feltville Formation, belongs to the simple scale group (sensu Olsen and others 1982).

Perhaps because specimens collected from Pompton seemed inferior (especially without preparation) to fishes from the already classic localities of Boonton and Sunderland or because Redfield described no new species, Pompton and this small collection of fishes never gained much notice. Neither Newberry (1888) nor Eastman (1905), in their reviews of fossil fishes from New Jersey, even mentioned that semionotids had been found at Pompton. Thus, little or no collecting had been done at Redfield's old locality until it was rediscovered by P. E. Olsen (Olsen 1975; see also Cornet 1977).

In 1979–80, the Yale P4 excavation yielded 1,900 semionotid fishes, including

at least 20 new species—far more than Redfield ever imagined. Although Redfield was right that fishes in the *S. tenuiceps* group (Redfield's *S. latus*) and the *S. elegans* group (Redfield's *S. fultus* and *S. agassizii*) are found at Pompton, most of Redfield's specimens and a major portion of all semionotids from cycle P4 are distinguishable from both groups.

Thirteen of these new species, described below, differ from European *Semionotus* in only minor ways—simple body proportions and some aspects of squamation, including slight deviations in the morphology of the dorsal ridge scale series. Six species from Pompton belong to the *S. tenuiceps* species group, which I argue is monophyletic. Two species belonging to the *S. elegans* species group are also found at Pompton, but these are being described, along with several other species, in a separate work.

To place the semionotid fauna from the P4 excavation into proper historical, paleontological, and evolutionary perspective, I briefly review the geology of certain aspects of the Newark Supergroup and of lake cycle P4. In the section on materials and methods, I include accounts of the procedures for excavation as well as systematic study because the semionotids for systematic study were collected with detailed stratigraphic data to allow later examination of the patterns of species distribution. As the primary purpose of this work is to describe species found in the P4 excavation, in the section on methodology considerable emphasis is placed on the process of grouping individuals into species, with special attention to problems inherent in the study of fossils such as incomplete or distorted specimens. Less attention is paid to the methodology for working out phylogenetic relationships; a cladistic methodology is assumed. After the systematic accounts, the general patterns of variation are reviewed and, inasmuch as is possible, comments on the relationships and classification of semionotids are offered.

2. GEOLOGICAL BACKGROUND

In the Late Triassic, a system of rift valleys developed near the eastern edge of the North American plate. This North American rift system was formed by the tectonic activity that eventually led to the opening of the Atlantic Ocean (Sanders 1974; Van Houten 1977; Manspeizer and others 1978). Intermittently, for about 45 million years during the Late Triassic and Early Jurassic, the rift valleys were occupied by large, deep lakes. The terrestrial and lacustrine sediments deposited in these valleys are included in the Newark Supergroup (Fig. 1; Olsen 1978).

Newark sediments have been a rich source of fossil fishes, tetrapods, invertebrates including insects, and both mega- and microfossil plant material. (For reviews, see Reeside and others 1957; Cornet and others 1973; McDonald 1975; Cornet 1977; Olsen 1980c; Schaeffer and McDonald 1978; Olsen and others 1978). Olsen and others (1982) used the distributions of fossil vertebrates, particularly fishes, to correlate sediments between major Newark Supergroup basins. Subsequently, this correlation was falsified by additional information about the distribution of fishes, leaving the desirable state of affairs that the presently preferred interbasin correlation rests on geochemical, paleomagnetic, and lithological data and is independent of the data on fish distributions (Olsen 1983).

The Newark Basin (Fig. 2), in central New Jersey and eastern Pennsylvania, is the largest of the Newark Supergroup basins, covering an area of about 8,200 km (Manspeizer and Olsen 1981). The long axis of the basin runs from Rockland County, New York, southwest to Lancaster, Pennsylvania, a distance of about 220 km (Olsen 1980b). At the southwestern tip of the basin, the terminal Robeson Conglomerate pinches out into the New Oxford Formation and Gettysburg Shale of the neighboring Gettysburg Basin (McLaughlin 1939). The eastern border of the basin is defined by the Hudson River in the north, and the basin is overlapped by Cretaceous rocks in the south. Major northeast-southwest trending faults running from Stony Point, New York, to near Reading, Pennsylvania, delineate the northwestern lateral border of the basin and separate the neighboring Paleozoic strata from the Newark Mesozoic rocks.

Six sedimentary formations and three basalt formations are exposed in the Newark Basin. In order of superposition, these formations are the Stockton, Lockatong, Passaic, Feltville, Orange Mountain Basalt, Towaco, Preakness Basalt, Boonton, and Hook Mountain Basalt (Olsen 1980a). Most of the exposed sediments in the basin are Late Triassic in age, including the Stockton arkose, the gray siltstones of the Lockatong Formation, and virtually all of the gray siltstones and red beds of the Passaic Formation. Early Jurassic sediments, including the Feltville, Towaco, and Boonton Formations (Cornet and others 1973), are exposed primarily in the Watchung Syncline in the northwestern portion of the basin (Fig. 2), with minor exposures farther west in the New Germantown, Jacksonwald, and Sand Brook Synclines (Olsen 1980a).

NEWARK SEDIMENTARY CYCLES AND ANCIENT LAKES

One of the most striking features of the gray siltstones in the Lockatong, Passaic, Feltville, Towaco, and Boonton Formations is that the pattern of their deposition was cyclic. Sedimentary cycles have been described in detail for the Lockatong Formation (Van Houten 1962, 1964, 1965, 1969; Olsen 1980b, 1984b), the



FIG. 1. Newark Supergroup of eastern North America (adapted from Olsen 1980b); A, Deerfield Basin; B, Hartford Basin; C, Newark Basin; D, Gettysburg Basin; E, Culpeper Basin.

Jurassic formations of the Newark Basin (Olsen 1975, 1980b), and in several formations in other Newark Supergroup basins (e.g., Olsen and others 1978). A generalized picture of Newark sedimentary cycles, taken primarily from Olsen and others (1978) and Olsen (1980b), is reviewed below.

Each sedimentary cycle consists of three units (Fig. 3). The lowest portion of a cycle, division 1, is composed of massive to platy and gray to black siltstones and sandstones. This unit often shows current bedding structures and contains burrows and burrow casts. Division 1 grades into the dark gray to black microlaminated pyritic siltstones, named division 2. The alternating laminae of light-colored carbonate-rich and darker organic-rich silt that comprise the microlaminations of division 2 are analogous to the annual varves found in the sediments of modern stratified lakes (Davies and Ludlam 1973; Olsen and others 1978; Olsen 1980b). The uppermost unit, division 3, is defined by the breakdown of the microlaminated structure of the sediments. Division 3 consists of gray, platy to massive mudstones that may be irregularly bedded and contain burrows, shrinkage cracks, ripple marks, and footprints (Van Houten 1964; Olsen 1975, 1980b; Olsen and others 1978).

Fossils occur throughout the cycle, but certain organisms and states of pres-

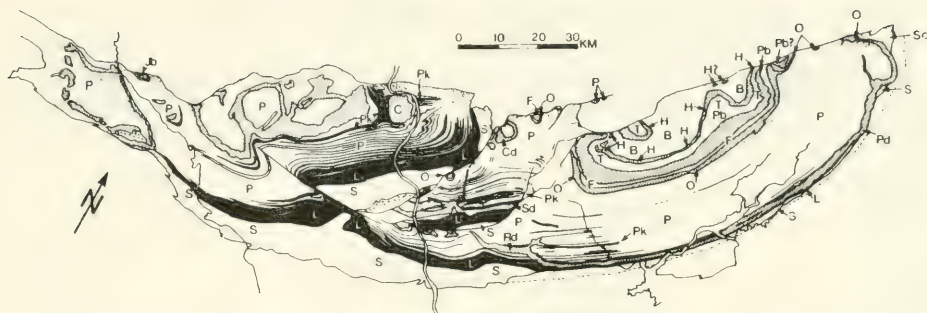


FIG. 2. The Newark Basin. Geologic map showing distribution of formations and conglomeritic facies (irregular stipple), and major clusters of detrital cycles in Passaic Formation (parallel black lines). Abbreviations of formations and diabase bodies as follows: B, Boonton Formation; C, Coffman Hill Diabase; Cd, Cushetunk Mountain Diabase; F, Feltville Formation; H, Hook Mountain Basalt; Hd, Haycock Mountain Diabase; Jb, Jacksonwald Basalt; L, Lockatong Formation; O, Orange Mountain Basalt; P, Passaic Formation; Pb, Preakness Basalt; Pd, Palisade Diabase; Pk, Perkasie Member of Passaic Formation; Rd, Rocky Hill Diabase; S, Stockton Formation; Sc, carbonate facies of Stockton Formation; Sd, Sourland Mountain Diabase; T, Towaco Formation (from © Paul Olsen, 1984, comparative paleolimnology of the Newark Supergroup: a study of ecosystem evolution. Ph.D. dissertation, Yale University).

ervation characterize different divisions of the cycle (Fig. 3). The best fossils, including fully articulated fishes and reptiles, conchostracans, ostracods, insects, and plants, come from division 2. Vertebrate fossils are also found in divisions 1 and 3, but they become progressively disarticulated farther away from the microlaminated sediments of division 2 (Olsen and others 1978; Olsen 1980b).

These Newark sedimentary cycles record the waxing and waning of very large, deep, stratified lakes (Olsen 1980b). According to Olsen's stratified lake model, each sedimentary cycle corresponds to the history of one lake episode. Division 1 was deposited during the lake transgression, leading to the development of a very large, deep, stratified lake. Division 2 was deposited during the deep-water phase. In these stratified lakes, the anoxic, H_2S -rich lower water layer was uninhabitable by burrowing organisms, scavengers, and other benthic biota. Absence of a benthic fauna and lack of physical disturbances allowed both the preservation of fully articulated vertebrates and fine sedimentary structure characteristic of division 2 (Twenhofel 1939; Olsen and others 1978; Olsen 1980b). The varve sequence of division 2 allows fish to be placed in a year-by-year chronology. The area of exposed microlaminated sediments for different Newark Basin lake cycles ranges from about 525–8,200 km². These figures are the minima of the areas of lakes that were deep enough (below the chemocline) to preserve varved sediments and undisturbed fossils. The lakes themselves must have been much larger, in some cases, perhaps as large as modern Lakes Tanganyika and Malawi (Olsen 1980b). Breakdown of laminations in the upper division of the cycle corresponds to the breakdown of lake stratification that occurred as the lake shallowed and finally evaporated. Mudcrack features and dinosaur footprints found high in the upper divisions of cycles were preserved during dry episodes.

The Newark Basin record includes a succession of approximately 220 discrete lake histories, separated by episodes when the basin was completely dry. By extrapolating from varve counts, periodicity of sedimentation was first estimated to be approximately 21,000–23,500 years (Van Houten 1969; Olsen 1980b) and corroborated by independent calculations based on radiometric dates and stratigraphic correlation (Olsen 1984a). Periodicity of lake formation and decline has been linked to the climatic changes induced by the precession cycle of the equinox and the eccentricity cycle of the earth's orbit (Van Houten 1969; Olsen 1984a).

GENERALIZED NEWARK SEDIMENTARY CYCLE

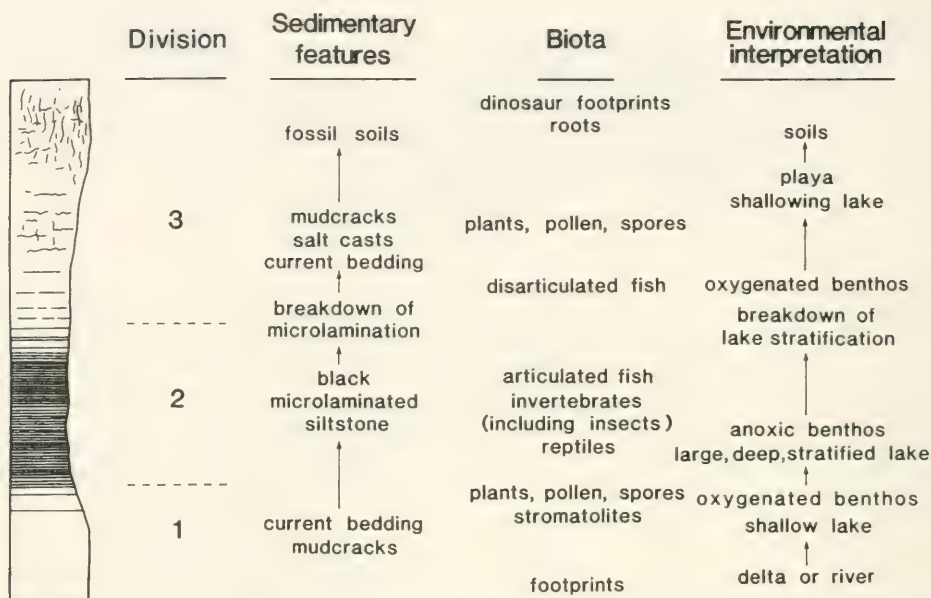


FIG. 3. Generalized Newark sedimentary cycle. A schematic stratigraphic section of a single Newark sedimentary cycle is pictured on the left. Divisions 1, 2, and 3 correspond to those described by Olsen (1980b). The corresponding progression of certain sedimentary features characteristic of each division of the cycle is listed in the second column. Characteristic fossils found in each division are listed in the column entitled "Biota." Together, the sedimentary features and character of the biota form the basis for the environmental interpretation of the stages of lake development given in right-hand column. As shown in the figure, one sedimentary cycle corresponds to the formation and evaporation of a single lake (for more detail see text; Olsen and others 1978; Olsen 1980b).

THE TOWACO FORMATION AND SEDIMENTARY CYCLE P4

The fishes described herein were collected by the author and others from an excavation in cycle P4 in the Early Jurassic Towaco Formation of the Newark Basin. Six Towaco cycles, composed of minor volcanoclastics and red, gray, or black sediments, have been traced throughout most of the Watchung Syncline (Olsen 1980a). The mean thickness of these cycles is 30–35 m, in contrast to the much thinner Lockatong cycles (1.5–5.2 m). The formation thickens toward the north near the Ramapo Fault to a maximum of 345–427 m and reaches its thinnest point (31 m) near Bernardsville, New Jersey, in the southwest (Cornet 1977; Olsen 1980a).

Towaco cycles have been described as having four main divisions (Olsen 1980b), the first three corresponding to those reviewed earlier. Conglomerates, gray siltstone, and sandstone make up division 1 of a Towaco cycle. These beds, characteristically showing cross-bedding and containing roots and reptile footprints, correspond to the transgressive phase of lake history. Division 2, consisting of gray to black microlaminated calcareous siltstone deposited during the deep-water phase of lake history, was the source for the semionotid fishes described in this work. Division 3 is a gray clastic unit similar to division 1 and represents the regressive phase of lake history. Division 4, a thick red clastic sequence of fining-upward cycles containing reptile footprints, roots, and mudcracks, is a fluvial, floodplain, and flood basin facies.

Towaco lakes filled a wedge-shaped basin, the deepest part being along the northwestern edge of the basin where the Towaco Formation is thickest (Olsen 1980b). As Towaco exposures are limited to the Watchung Syncline, the area of microlaminated sediments of cycle P4 is 526 km². The actual lake may have been as large as 8,000 km² and as deep as 200 m (Olsen, personal communication).

3. MATERIALS AND METHODS

Semionotid fishes have been collected from a number of Newark Supergroup localities by both amateurs and professionals for well over a century. As a result, many museums in the United States and Great Britain have collections of Newark semionotid fishes from the well-known localities in Boonton, New Jersey; Sunderland, Massachusetts; and Durham, Connecticut. Of particular note are the following: Newberry's collection at the American Museum of Natural History; Eastman's collection at the New Jersey Science Museum and at the Museum of Comparative Zoology; the Redfield Collection at Yale Peabody Museum; Hitchcock's collection at the Pratt Museum, Amherst College; and Loper's collection at Wesleyan University and the U.S. National Museum. These collections provided a rich source of material for recognizing the morphological variability of semionotids initially and then for working out their basic morphology (Olsen and McCune ms). However, as specimens in existing collections lacked the fine-scale stratigraphic data that one would like to have for evolutionary studies, a new collection of semionotids was made in which the microstratigraphic position of each fish was recorded. Study of the species-level systematics was begun on the fishes for which there were stratigraphic data; however, all species determinations were made independently of stratigraphic data.

EXCAVATION

The excavation site in cycle P4 of the Towaco Formation was chosen for several reasons. Existing material in the Yale Peabody Museum and the American Museum of Natural History indicated that the Early Jurassic faunas in the Newark Basin were particularly diverse. Of known Early Jurassic localities, Redfield's Pompton locality was attractive because 1) three successive lake cycles are exposed there, affording the opportunity to track the faunas in temporally successive lakes, and 2) many of the fish could be easily prepared by negative preparation in acid (see below). Excavation of cycle P4 included the beds discovered by W. C. Redfield (1843) at Pompton, New Jersey. These beds correspond to division 2, cycle P4 of the Early Jurassic (Hettangian) Towaco Formation in the Newark Basin of New Jersey (see Olsen 1980a). The exact geographic location of the excavation is recorded in the catalog of the Peabody Museum of Natural History, Yale University, but by agreement with the owners of this property this information will remain unpublished.

Excavation in Towaco cycle P4 proceeded as follows: The overburden was cleared from an area larger than the area designated for excavation. A dinosaur footprint, roots, and plant material were collected in the uppermost sediments, designated as division 3. Lower in the cycle but still above any microlaminated sediments, meticulous collecting began when fossils were found with reasonable frequency, about 20 fossils per cubic meter (mostly plants and very rare scrappy fish). Meticulous collecting involved a systematic search for fossils across the entire area of the excavation (about 3 m²) one layer at a time, a layer being from 1–3 cm thick. All fossils found were collected regardless of taxonomic identity, completeness, or quality. Collecting continued through microlaminated division 2 of the cycle (about 3 m) to a point below where fish fossils appeared to be absent.

Fish were found by splitting the pieces of each slab into thin laminae (1–100 mm, as was possible). The rock often split along a bedding plane containing a fish, presumably because of the different weathering properties of bone and rock.

Some fish were not exposed on a bedding plane but were seen as slight bulges under a thin layer of matrix. When fish were not found by splitting rocks along the bedding plane, the rocks were broken into small pieces in order to look for fish in cross section. Fish can be seen in this way because the rock matrix is light gray, weathering to tan or light brown. In contrast, the bone is black and thick enough to be visible in cross section as a black lens. Fossils found in cross section or under a thin layer of matrix were collected without exposing the fossil further.

While still in the field, fish were reassembled and fitted back into the layer in which they were found. This tedious operation served two purposes. It forced the collector to orient the specimen correctly relative to both the "up" surface (for stratigraphic purposes) and north (for taphonomic purposes). Second, as it forced the collector to reassemble all pieces of a fish, it was the best way to find any fish remaining in situ or to discover that some pieces of fish that had already been discarded needed to be found. Each specimen was given a field number with the prefix P4. The number, description, and microstratigraphic location of each specimen were entered into the field notes.

Excavation proceeded through two seasons in two adjacent vertical passes through the same fish-bearing unit. There were not enough obvious marker beds to relocate the same micro-units reliably in the field, so in both field seasons a reference sample was collected for every micro-unit. Reference samples were also given field numbers, and these numbers were recorded in the field book along with the micro-unit name and a lithological description. These reference samples—cut, polished, and assembled into two columns—relate the microstratigraphic positions of fish collected in different seasons.

The method of "peeling off" sediments layer by layer and recording the microstratigraphic unit or location for each fish probably gives stratigraphic detail as fine as one would want. However, it is possible to determine relative positions of the fish even more precisely by matching the microlaminations on two fish-bearing rocks in a given micro-unit. Similar microlaminations in other Newark sediments (Lockatong Formation) have been matched successfully over a distance of 15 km (Olsen 1980b), although such long-distance microcorrelation would be hampered in Towaco cycle P4 near the excavation because these beds are frequently slumped and fragmented by microfaults.

THE FOSSILS

Two thousand one hundred fifty fossils were collected in two summers. Seven percent of these are plants, about 5% are unidentified scraps, and the remaining 88% are semionotid fishes. No fishes but semionotids and no other vertebrates except a single dinosaur footprint (not in the fish-bearing unit) and an isolated tetrapod vertebra were found. Most of the fishes are small, about 7–12 cm, although the total size range is quite large, from about 6–30 cm. Except on one particular bedding plane, where there were six similarly sized fish preserved together (YPM 8813) on a slab of rock about 225 cm², there is no indication that the fishes in these sediments died of a common cause or at a common time. Few individuals show evidence of being mouthed by predators. Whatever the causes of death, the fishes appeared to be scattered without apparent pattern throughout the section, at a density of roughly five to six fish per centimeter of sediment over the 3-m² area.

Virtually all fish are laterally compressed and preserved in lateral view. Throughout the section, most are fully articulated (though many were not suc-

cessfully collected and prepared as complete fish owing to weathering, faults, physical limits of the excavation, etc.). The bone of most fishes is black and is thus easily visible in contrast to the unweathered light gray matrix or weathered tan matrix. These fishes may be as thick as 2–3 mm and are thus visible in cross section as a black lens of bone. Other fishes are preserved as very thin, brown impressions in weathered yellow powdery matrix. These fish are the most difficult to find and are often too poorly preserved to yield much morphological information.

PREPARATION

No single method of preparation suits all fish from the P4 excavation. When possible, the preferred method of preparation was to expose the fish completely and then dissolve the exposed bone but not the matrix in hydrochloric acid, leaving a negative mold of one or both sides of the fish. Next, the specimen was hardened with very dilute glyptol and cast in latex for study. The internal skeleton is poorly ossified in these fishes and generally not preserved, so that negative acid preparation only destroys the dermal skeleton. Detail of the dermal skeleton is better seen from a cast of the prepared impression than from the bone itself, because what is usually visible in the latter is an irregular median section of the scales or skull bones rather than the external surface. Because negative preparation destroys the bone, before preparation in acid, flank scales were removed and saved for later thin sectioning. For this purpose, small blocks of cured epoxy were glued onto scales with fresh epoxy. When the fresh epoxy was completely cured (1–2 days later), the block was pulled off the specimen with pliers. In most cases, the scales from both sides of the fish remained glued to the epoxy block, leaving a perfect negative mold in the rock and the scales conveniently glued to the epoxy block for further embedding and sectioning.

Negative preparation was not possible on relatively weathered rock or where the exposed lamina was high in calcium carbonate. When it was not possible to prepare fish in acid, it was usually possible to prepare specimens mechanically with an aircscribe, an airbrasive machine, or, most effectively, a thin-bladed (no. 11) scalpel.

SAMPLING

From the state of preservation of these fishes and from their paleolimnological context, we can begin to identify the strengths and weaknesses of the collection as a representative sample of the P4 fish fauna. To do this, we must consider two aspects of sampling. First, what is the relationship of the sample of fishes from the Yale P4 excavation to all the fishes preserved in the record of cycle P4 in the Newark Basin? Second, what is the relationship between the taxonomic composition of fishes in the P4 fossil fauna to its once living counterpart?

Within the local Pompton area, only physical accessibility determined the specific site for excavation. Presumably, the fauna would be equally diverse anywhere in the Pompton cliff exposures. In similar Lockatong sedimentary cycles, the faunal composition within cycles is constant over a distance of 15 km or more (Olsen 1980b). Thus, we can probably assume that the sample is arbitrary, if not random. This assumption could be tested by sampling the cycle laterally.

Although the sample of the P4 fossil fauna may be arbitrary, the fossil sample of the living community could not have been arbitrary. Larger samples of cycle

P4 could not overcome these biases. However, the paleoecological circumstances of preservation in a large meromictic rift lake may have produced an unusually fair picture of the once living fish fauna. I will discuss this in a limited way below, but it should really be the subject of a separate taphonomic study.

As discussed earlier, the microlaminated sediments were deposited in the anoxic lower waters of a stratified lake. An important taphonomic feature of the P4 fauna is that articulated fishes predominate throughout this microlaminated division of the cycle. This pattern contrasts with the pattern in some Lockatong cycles (W5, W6) where the proportion of disarticulated material gradually increases from division 2 toward both divisions 1 and 3. These different taphonomic patterns may be due to differing basin topographies. Although both localities are near the edge of the basin, the sediments may have been deposited in the deepest part of a wedge-shaped basin (Olsen 1980b), where stratification (and the anoxic benthos preserving articulated fish) would have persisted through minor fluctuations in lake level and for the longest time over the history of the lake.

An anoxic lake bottom at a depth of 100 m or more could not have been the habitat of these fishes; at the very least, they must have been transported down from the epilimnion. If the semionotids collected from P4 inhabited shoreward habitats, they must have been transported at least a moderate distance to the area of the lake deep enough to produce laminated sediments. If this were the case, transport of fish by a geographically localized current could have biased the sample toward fishes from a particular nearshore habitat type, but casual observation at least suggests that there is no preferred orientation of the fishes relative to the "north arrow" marked on each specimen. (Data to test this assumption are being collected.) It seems likely that the preservation of fishes on an anoxic lake bottom would be biased toward open-water fishes more than fishes from nearshore habitats. At best then, the apparent diversity of P4 fishes is much lower than the real diversity of the P4 lake, simply because the nearshore fishes are probably under-represented.

Another way to think about the relation of this sample of fossils to the once living community is to ask the hypothetical question: How representative a sample of fishes could one get by setting a net in the muck at the bottom of Lake Malawi and retrieving the catch once a year? Although very coarse, this sort of sampling could detect the relative diversity of fishes in Lakes Malawi and Superior. In this hypothetical sampling program, long-term sampling could compensate partially for geographic limitations. Similarly, the interval of 5,000–7,000 years covered by the P4 sample may compensate for the lack of geographical diversity of sampling areas, assuming that species composition in the lake changed little either by evolution or by community population dynamics during that time.

MEASUREMENTS AND COUNTS

I took a variety of measurements, which reflect overall body shape (Fig. 4). Most of these follow Hubbs and Lagler (1947), but I have added several less conventional ones, such as the distances between the dorsal fin and pectoral fins, the dorsal fin and the pelvic fins, and the dorsal and anal fins. Most measurements are distances between morphological landmarks.

The most reliable and efficient way to take measurements was to isolate morphological interpretation from the process of measurement. To this end, I located morphological landmarks using a Wild M5 dissecting scope and then marked a small dot of water-soluble paint on the landmark. This procedure supplied the

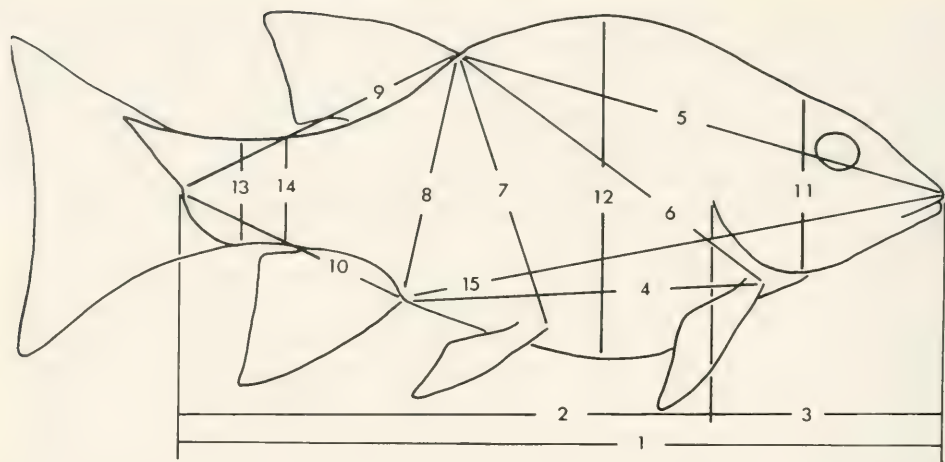


FIG. 4. Measurements. Numbers correspond to the following measurements, described in the text: 1, SL; 2, BL; 3, HDL; 4, PTAL; 5, PDL; 6, DFPT; 7, DFPV; 8, DFAN; 9, DFCD; 10, AFCD; 11, HDD; 12, DPTH; 13, MINCD; 14, MAXCD; 15, PAL.

magnification necessary for interpreting the morphology of the fossil while at the same time allowing a wider angle of view (without the scope) for measurement. A similar technique of using the dissecting scope to mark individual scales and then counting the marks without the scope was the most reliable way to count scales. All measurements were made to the nearest millimeter using dial calipers or, for larger fishes, a steel centimeter ruler. The following measurements were taken for each specimen (see also Fig. 4).

ABBREVIATIONS AND DEFINITIONS FOR MEASUREMENTS

BL	distance from the posterior margin of cleithrum to the base of the axial lobe of the heterocercal tail (a sort of inflexion point in the outline of the scaled portion of the tail)
SL	distance from the anterior tip of the snout to the base of the axial lobe of the heterocercal tail
PTAL	distance between the origins of the anal fin (base of the first fulcrum) and one of the pectoral fins
HDL	distance from the tip of the snout to the posterior margin of the cleithrum, along the axis of the parasphenoid
DFB	length of the base of the dorsal fin; from the base of the first fin fulcrum to the base of the most posterior lepidotrichium
AFB	length of the base of the anal fin; from the base of the first fin fulcrum to the base of the most posterior lepidotrichium
PDL	predorsal length; distance from the tip of the snout to the base of the first fulcrum of the dorsal fin
PAL	preanal length; distance from the tip of the snout to the origin of the anal fin
DFPT	distance between the origin of the dorsal fin and one of the pectoral fins
DFPV	distance between the origin of the dorsal fin and one of the pelvic fins
DFAN	distance between the origins of the dorsal and anal fins

DFCD	distance between the origin of the dorsal fin and the base of the axial lobe of the heterocercal tail
AFCD	distance between the origin of the anal fin and the base of the axial lobe of the heterocercal tail
DPTH	maximum body length
HDD	head depth from the posterior edge of the parietals to the ventral border of the cleithrum
MINCD	minimum depth of the caudal peduncle
MAXCD	maximum depth of the caudal peduncle

COUNT ABBREVIATIONS AND DEFINITIONS

Scales

VDSC	number of scales between the lateral line and the origin of the dorsal fin
VVSC	number of scales between the lateral line and the origin of the anal fin
PLVSC	number of lateral line scale rows anterior to the pelvic fins
ANFSC	number of lateral line scale rows posterior to the postcleithral scales and anterior to the base of the first fulcrum of the anal fin
DFSC	predorsal scales; number of lateral line scale rows posterior to the postcleithral scales and anterior to the base of the dorsal fin
CDSC	number of lateral line scales, beginning with the first scale posterior to the postcleithral scales and ending with the scale at the base of, but not including, the scales in the axial lobe of the tail
AXSC	number of scales from the base of the axial lobe of the tail to the tip, counted one vertical scale row in from the posterior edge of the tail
DRS	number of dorsal ridge scales

Fin rays

PCTR	number of lepidotrichia in one pectoral fin
PLVR	number of lepidotrichia in one pelvic fin
ANFR	number of lepidotrichia in the anal fin
DFR	number of lepidotrichia in the dorsal fin
CDDR	number of caudal lepidotrichia dorsal to the lateral line
CDVR	number of caudal lepidotrichia ventral to the lateral line

Fin fulcra

DFF1	number of basal fin fulcra, dorsal fin
DFF2	number of basal fin fulcra plus those that lie against the unsegmented portion of the first lepidotrichium, dorsal fin
DFF3	total number of dorsal fin fulcra
AFF1	number of basal fin fulcra, anal fin
AFF2	number of basal fin fulcra plus those that lie against the unsegmented portion of the first lepidotrichium, anal fin
AFF3	total number of anal fin fulcra
PCTF	number of pectoral fin fulcra
PLVF	number of pelvic fin fulcra
CDF	number of dorsal caudal fin fulcra
CVF	number of ventral caudal fin fulcra

RELIABILITY OF MEASUREMENTS

Measurements between distinctive morphological landmarks, like the origin of the dorsal and anal fins, were more repeatable. The least reliable measurements were head depth (HDD) and pelvic fin distance (DFPV), because the cleithrum and pelvic fins had often shifted during preservation. To a lesser extent, measurements involving the tip of the snout and the origin of the pectoral fins are more variable in these fossils than they were in life owing to slight disarticulation of the premaxillae and separation of the pectoral fins from the shoulder girdle. Consequently, the measurements HDD, DFPV, MAXCD, and to a lesser degree HDL and DFPT are probably more variable within the fossil species than they were in the corresponding living species.

Counts of fin rays may be low when fins were not preserved fully spread. Meristics of median fins are more reliable than those of paired fins, as the former are usually far better displayed and preserved.

THE PROBLEM OF DISTORTION

As measurements of overall body form figure prominently in the taxonomy of Newark semionotids, it is important to comment on the possibility that different shapes of fossil fishes are not biologically real, but diagenetically produced.

Diagenetic distortion of both fish and rock occurs in at least some individuals, but distortion cannot explain the variation in shape. If diagenesis were the cause of shape variation, we would expect all types of fishes from a given locality to show a similar range of variation in shape. In another Jurassic lake deposit in the Newark Basin (Boonton, New Jersey), there are three non-semionotid fish genera, but only semionotids vary noticeably in body shape. Similarly, not all groups of semionotids at Pompton include the same range of shapes, but this pattern is not as obvious at Pompton as it is at Boonton because the groups at Pompton are so closely related.

Two kinds of distortion might affect our assessment of shape variability. Distortion of both fish and rock may occur during diagenesis. Postmortem distortion of the fish before fossilization may include varying degrees of disarticulation, bent or twisted fins, injury due to scavenging or predation, and change in form owing to the translation of a three-dimensional fish into a two-dimensional fish.

Distortion occurring during diagenesis is apparent in both the fish and in the fabric of the rock. Microfaults are fairly common and may slightly or more radically displace two parts of a fish. Fishes in slumps are distorted in proportion to the rock itself and may be folded, wrinkled, or just mildly misshapen. It is easy to recognize these diagenetically distorted fish and eliminate them from analysis.

What kind of distortion occurs in the process of "flattening" a fish? Semionotids have an exoskeleton of rigid, interlocking, ganoid scales bound together by a fabric of collagen fibers. Translation of the three-dimensional fish to a two-dimensional fish probably occurs in one of two ways. The exoskeleton—essentially a cylinder of scales—may be flattened, so that the depth of the fossil fish is roughly equivalent to the body depth plus half the width of the living individual. This manner of flattening would present no problem for using shape as a taxonomic character. Measurement of body depth in the living fish and corresponding fossil would be different, but as only fossils are being compared with fossils, measurements should be comparable. Alternatively, a three-dimensional fish might "collapse" into a two-dimensional fish like a concertina. In this case, flattening would be accom-

plished by imbrication of the flank scales and the outline of the fish would be more or less preserved. Again, measurements would be comparable. (However, measurements of fish in different preservational regimes may not be comparable, as for example between Newark semionotids and those that are preserved three-dimensionally—e.g., from the Karoo Formation of South Africa.)

In the two living fish with similar scales, *Polypterus* and *Lepisosteus*, there is more flexibility between vertical scale rows (the direction of flexibility necessary for swimming) than between horizontal scale rows (Pearson 1981). Thus, if translation from three to two dimensions occurs by collapse rather than flattening, we would expect the vertical scale rows to imbricate in an anterior-posterior direction, especially in the anterior trunk region, where the fish is thickest. If this is how translation occurs, then the measurements would not only be comparable among fossils but comparable between a fossil and its living precursor.

Both flattening and collapsing probably occur. Collapsing is suggested by the fact that scales in the central anterior flank region but not the caudal peduncle tend to be imbricated in the fossils and the fact that the dorsal midline of the living fish, marked by the dorsal ridge scales, always marks the dorsal edge of the fossil. Some flattening is suggested by the usual extension of the belly (presumably up to one-half its width) below the insertions of the paired fins. The important point, however, is that the preservation of Newark semionotids as two-dimensional fossils from three dimensions appears to occur in the same way.

ABBREVIATIONS FOR INSTITUTIONS

AMNH	American Museum of Natural History
BMNH	British Museum (Natural History)
MNHP	Museum d'histoire naturelle Paris
YPM	Yale Peabody Museum
BGS.GSM	British Geological Survey, Geological Survey Museum (formerly Geological Society of London)

4. METHODOLOGY

The primary goal of this work is to describe the variability in semionotids from the P4 excavation and to use that variability to recognize species. Advancement of a phylogenetic hypothesis for the species described here is an eventual but not immediate goal. Hence, the following discussion of methodology places greater emphasis on grouping individuals into species than on analyzing the cladistic relationships of those species. My approach to grouping individuals was tailored to general problems inherent in the study of fossils and to specific problems of analyzing the Semionotidae.

An unusual aspect of the problem of sorting these semionotids into species (more conservatively, morphotypes) is that there was no starting organization from which to work. More than 15 species have been described from eastern North America (Woodward 1895; see also Newberry 1888; Bock 1959), but these early descriptions are too vague to be useful for identification. The result is that most of the holotypes of semionotids from eastern North America do not represent a well-formulated concept of a particular species. Comparisons of the holotypes of species described in the nineteenth century with fishes from Pompton reveal that all but one of the Pompton species are distinguishable from previously described species. The advantage of this circumstance is that the taxonomic analysis of the semionotids from cycle P4 must start afresh; history cannot prejudice the outcome. On the other hand, the analysis has not benefited from the insights of previous workers.

SHAPE, FORMING GROUPS AND HYPOTHESIS TESTING

The most obvious variation in semionotid fishes from Towaco cycle P4 and many other Newark cycles is variation in body shape. The range of variation is comparable to that in some of the largest families of freshwater teleosts (such as cichlids or characins), but in the past only three poorly described species of *Semionotus* have been recognized from Pompton. For living fishes, body shape is more commonly used for descriptions than diagnoses, although it is certainly used implicitly for initial sorting. This is not to say that ichthyologists do not take continuous measurements or analyze them; less subtle and more readily analyzed characters are simply preferred when they are available.

Elsewhere I have made the argument that although fishes having the same shape need not be the same species, fishes with different shapes are very likely not the same species (McCune 1981). It is on that premise that I began to sort this closely related complex of species by body shape. My assumption was that non-shape characters may define subsets of similar shapes; they do not define groups of heterogeneous shapes.

The principal problems in the operation of grouping individuals by shape were 1) to represent and compare shapes objectively and 2) to include information about incomplete specimens without diminishing confidence in the results by including estimated or ambiguous data. In doing the analysis, these two general problems were inseparable. The solutions on a methodological level (trivial hypothesis testing) and on an operational level (camera viewer technique, system of measurement, and quantitative analysis), as discussed below, were the same for both problems.

Morphological data are difficult to collect unless one has an idea of what to

look for. This is especially true for fossils in which sutures and cracks must be distinguished, but it is probably true at least to some degree for living organisms. At worst, this statement can be translated as "one sees what one wants to see," and certainly even investigators with the greatest integrity have seen more in their specimens than actually existed (see comments on a much larger version of the same problem by Patterson 1981). However, looking for particular morphologies seems more respectable if it is couched in the jargon of the hypothetico-deductive method: The best way to see morphology of a fossil is to test each new fossil against a previous idea—the interpretation of a fossil one has previously examined. Although application of the methodology may seem trivial, the same logic is useful for grouping individuals by shape in an analogous way to specifying "seeds" to an agglomerative clustering algorithm: It is also a useful logic for incorporating data from incomplete specimens into the analysis. Because the line between subjectivity and objectivity is potentially fuzzy, I detail this methodology below.

For incomplete specimens, my methodological procedure assumes that in any given individual a character has the common state, unless proven otherwise. Falsification most often comes from another character. An example would be as follows: Suppose an individual **X** from Pompton was clearly a non-*Lepidotes* semionotid, but the morphology of its dorsal ridge scales was ambiguous. I would hypothesize that this individual had simple, convex dorsal ridge scales and tentatively include it in *Semionotus*. This is simply a probability statement based on the most common dorsal ridge scale morphology of semionotids at Pompton. (When grouping individuals, the least harmful hypothesis is based on probability; if one were making a similar argument for determining relationships, the least harmful hypothesis would be to assume primitive unless proven derived.) If, in the process of grouping individuals of *Semionotus* by shape, fish **X** did not fit into a category defined by a fish with definite simple convex dorsal ridge scales, then I would reject the interpretation that fish **X** has simple dorsal ridge scales and look to see if its shape resembled one in another dorsal ridge scale group. A new shape group with simple scales could not have been defined by an individual in which either shape or dorsal ridge scale morphology was ambiguous, but had fish **X** fit into an already existing shape group of simple-scaled fishes, then its scale counts, fin ray counts, and so forth could be included in a description of intraspecific variability. If the knowable morphology of fish **X** was consistent with two or more categories, the fish would not be referred to any group.

This procedure ensures that no new groups will be formed by ambiguous information (analogous to insurance against being found guilty when innocent in law or a Type I error in statistics), but it is possible to err by including an individual in a group where it does not belong, the worst consequence being a distorted picture of intraspecific variability. However, if fish **X**, with ambiguous dorsal ridge scales, were a gross outlier in any other character, I would set it aside as indeterminate until it was found to be consistent for all available characters with a given species.

In summary, my basic methodology for grouping individuals into species has been a mental iteration of formulating and testing a series of trivial hypotheses about morphology. It is a method that is as philosophically respectable as the hypothetico-deductive method and as analytically respectable as specifying a seed to a clustering algorithm.

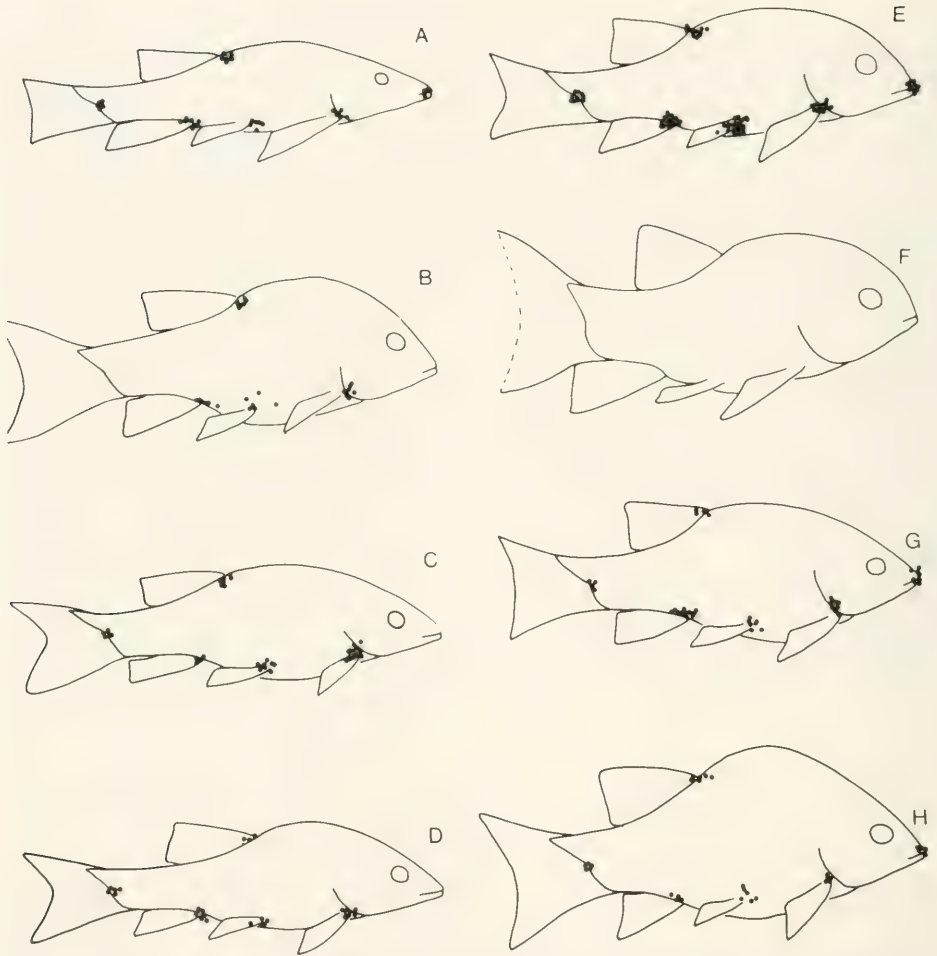


FIG. 5. Morphotype-variability plots representing the shapes of eight groups that correspond to species described here. A, *S. kirschi*; B, *S. olseni*; C, *S. virginiae*; D, *S. thomsoni*; E, *S. euthenius*; F, *S. convalis*; G, *S. redfieldii*; H, *S. schaefferi*. The outline for each species is a tracing from an individual specimen (in most cases, the holotype). For each additional specimen considered, the overall shape (at a standard size) and fin positions were superimposed (see description in text) and morphological landmarks were plotted on the original tracing. Thus, B represents a single individual while H represents variation in shape and fin positions of seven individuals. Morphological landmarks recorded for each fish were anteriormost tip of snout; origin of dorsal fin; base of the axial lobe of the tail; origin of pelvic fin (left or right depending on the orientation of the fish); and origin of pectoral fin (left or right depending on the orientation of the fish). Drawings all standardized for standard length.

GROUPING BY SHAPE

The most useful tool for sorting these fishes by shape was a Goodkin viewer. A Goodkin viewer projects an enlarged or reduced image of an opaque object, such as a fossil, onto a drawing surface. With the aid of this viewer, tracings of individual fish were easily standardized for size and then grouped by shape. In doing so, my assumption was that shape changes little as a function of size over the relevant size range (7–12 cm).

My procedure for grouping was to begin with the shape of one individual and test successive shapes against it as follows: I chose a well-preserved fish and using the Goodkin viewer traced its outline and marked the origins of its fins on tracing paper. I then put another fish under the viewer and compared it with the tracing

of the first. For the most part, fish were either obviously the same or they were obviously different. In only a few instances did complete fish seem "intermediate." When a new fish matched a tracing, I marked the positions of its fins on the original tracing. When a fish did not match a tracing, I made a new tracing for that particular fish. The final result was a group of tracings (Fig. 5), each one with a scatter plot of the positions of fin origins—what one might descriptively call a "morphotype-variability plot."

These fish-to-tracing comparisons are multivariate because the positions of all the fins, the distribution of body mass about the lateral line, the general form of head and tail, the slope of the forehead, and so forth must all match at once. Furthermore, if two fish are not the same shape, then how they differ is readily apparent. Of course, within species there are certainly variations in the relations of all these aspects of form; but in practice, while allowing for variability, there seems to be a quantum difference in shape and fin position (they are inseparable here because fin positions are used as homologous points to describe shape; cf. Humphries and others 1981) between what I would recognize as two distinct forms. A comparison of this sort is the geometrical analogue to cluster analysis, in which the goal is to partition a heterogeneous group into subgroups that have small within-group variances relative to the between-group variances.

A particular advantage of the Goodkin viewer technique is that judgments about shape similarity can be made using the entire perimeter of a form, not just the rough approximation of that form represented by a few measurements. Most measurements depend on the availability of natural landmarks such as the origin of a fin or the tip of a snout. Therefore, the quality of a mathematical representation of a form depends on the distribution of landmarks on that form. For these fishes, the distribution of landmarks is sparse in some critical areas, such as along the curvature of the body anterior to the dorsal fin and posterior to the head. In addition, the number of operationally available landmarks is often reduced by the vagaries of preservation, collection, and preparation, though the outline of the fish may remain intact.

After grouping the fish by shape with the viewer, I superimposed pairs of tracings with scatter plots of fin position in order to discern what aspect of shape formed the basis for grouping. In several cases, I merged groups because the fin scatter plots of the groups were overlapping and therefore indistinguishable.

QUANTITATIVE ANALYSIS OF SHAPE AND INCOMPLETE SPECIMENS

Given these viewer groups, the next step was to specify the differences between groups quantitatively. The obvious solution should come from one of the techniques of multivariate analysis, but here the abundance of incomplete specimens was a problem. Most multivariate analyses require that missing data be estimated or that any case containing a missing value be omitted. Estimating data is not a practical solution. When the problem is to discover homogeneous subgroups within a larger heterogeneous group, ordinary techniques of estimating missing data (inserting means, using regression statistics, etc.) may homogenize the heterogeneous subgroups. Omitting incomplete cases was undesirable because of the resulting drastic reduction in sample sizes. Tailoring measurements to minimize missing values is one possible solution, but it is hampered because there are relatively few morphological landmarks on a fish that can be used as endpoints when measuring shape.

One might devise a system of measurement that generates new reference points from landmarks that are usually present in incomplete specimens or that are based on less precise though important features of a form (such as the point along the dorsal midline where the body is maximally deep). I have devised one such system (McCune 1981). However, using these measurements alone, I was unable to discover satisfactory groups; I found that the difficulty of detecting and characterizing differences in fish shape is aggravated by less precisely defined landmarks and that these differences are swamped out by the variability of those measurements. Therefore, I relied on traditional measurements (see Chapter 3) and direct geometrical comparisons using the Goodkin viewer, the latter being especially important for incomplete specimens.

With the viewer, maximum available information for each individual can be included in the primary stages of grouping even though a specimen is incomplete. The desirable result is that the groups may be based on many more specimens than they would be if only complete specimens were used. The subsample of complete specimens in these Goodkin viewer groups was then described quantitatively by a stepwise discriminant function (BMDP7M; Dixon and Brown 1979) in order to analyze the morphological basis of shape classes and to calculate a classification function for placing additional individuals into these groups. Unless the variability within Goodkin viewer groups is significantly different from the variability in the subgroups analyzed quantitatively, it does not matter that the discriminant analysis is based on fewer specimens. My justification for using only the viewer outlines when numbers were inadequate for quantitative analysis is that with greater numbers, the viewer groups can be recognized and described quantitatively by a discriminant function. Since the two techniques give consistent results when both can be used, then when low numbers prevent the use of one (discriminant analysis) the other (Goodkin viewer) may be used with some confidence.

The discriminant analysis was used to describe different shapes and to identify important discriminating variables. Although the classification functions from this analysis are included in species descriptions, for operational taxonomy, regression equations are probably more useful. Therefore, in the species descriptions I include summary statistics and regression equations calculated by using the least squares method (SAS or Statistical Analysis System; Helwig and Council 1979) for each variable.

Subsequent to the completion of this work in 1982, a variety of sophisticated methods for describing and analyzing shape were published (e.g., Bookstein and others 1985; Ferson and others 1985; Siegel and Benson 1982). The interested reader may wish to consider these.

SYSTEMATIC METHODOLOGY

After species determinations were made, the relationships of these species were analyzed using a cladistic methodology (Eldredge and Cracraft 1980; Nelson and Platnick 1981; Wiley 1981) derived from that formalized by Hennig (1966). Groups were defined on the basis of synapomorphies, recognized through outgroup comparisons. Ontogenetic data were not available to help determine polarities. Given the set of characters and polarities, the cladogram requiring the fewest ad hoc assumptions about character transformations is presented in Chapter 8. Implicitly, some characters were weighted by the manner in which they were coded and by the omission of other characters. For example, in this analysis, shape was

implicitly weighted by being coded as a single character. Ganoine reduction on dorsal ridge scales was devalued relative to other characters because it is a common trend in actinopterygian evolution. The rationales for these and other decisions regarding the analysis of particular characters are explicated in Chapter 8. The proposed cladogram is viewed only as a statement about the distribution of synapomorphies in this group of taxa. It is hoped that the addition of more information about characters, taxa, geographic and stratigraphic data, and perhaps even ontogenetic data will improve the cladogram and aid in the reconstruction of a genealogy.

5. QUANTITATIVE ANALYSIS OF THE SIMPLE SCALE GROUP

A discriminant analysis was used to describe the general shape of species having simple or modified simple dorsal ridge scales. In other species, multivariate analysis was either not possible because the number of individuals was too low, or the analysis was unnecessary because some other character distinguished that group from the most similar groups.

Below, I discuss the results of the discriminant analysis for eight groups defined by the Goodkin viewer analysis. Seven of these "species" have simple, convex dorsal ridge scales. The eighth, *Semionotus schaefferi*, which has modified simple scales, was included in the morphometric analysis because there were sufficient numbers of specimens to do so, and the taxonomic significance of the dorsal ridge scale modification was unclear.

One hundred eighty fishes were grouped by shape according to the Goodkin viewer technique described earlier. The resulting morphotype-variability plots for the seven groups are pictured in Figure 5. The outline is not a reconstruction but rather a tracing of a representative individual, usually the holotype of that species.

The Goodkin viewer groups were then described quantitatively by a stepwise discriminant analysis (BMDP7M; see Dixon and Brown 1979) of the measurements listed in the section on materials and methods. Of the 17 measurements taken, I excluded BL from the analysis because it equals the difference between SL and HDL. I also excluded DFB and AFB because they were difficult to measure reliably on many specimens. For the discriminant analysis, I used 13 measurements: PTAL, HDL, HDD, PDL, PAL, DFPT, DFPV, DFAN, DFCD, DPTH, AFCD, MAXCD, and MINCD, all percentages of standard length, which at least approximately standardizes the measurements for size. I did not standardize the ranges of variables by transformation, because the actual ranges of all variables except the caudal peduncle depths differ very little. Individual cases missing any values were omitted from the analysis. Therefore, of the 180 fish sorted by the Goodkin viewer technique into eight groups, only 58 fish (spread across all eight groups) were included in the analysis.

The first run of the discriminant analysis correctly classified 93% of all individuals according to the discriminant function based on my eight original groups (Table 1). Misclassifications included several distorted fish (which I deleted from the final run), several measurement or recording errors, and two fish not having simple dorsal ridge scales. In two cases I switched a misclassified fish from one group to another.

The final run correctly classified 98% of the individuals. The BMDP program also includes a "jack-knife" option in which a classification function is recalculated for the specified groups less one individual in each group. The omitted individuals are then reclassified according to the jack-knife classification function. The percentage of incorrect assignments for each group gives a measure of the probability of error in future assignments (Neff and Marcus 1980). Obviously, small groups are likely to be more subject to error if an individual is omitted from the calculation. In the jack-knife classification, 75–100% of the individuals in each group were correctly reclassified. Considering the relatively small number of individuals per group (55 in the 5 largest groups), the jack-knife classification showed that the larger groups are relatively stable.

The first canonical variable of the discriminant function, which accounts for 60% of the total variance, is principally a composite depth variable. It is most

Table 1. Classification functions*

VARIABLE	A	B	C
SPTAL	45.06207	47.55438	43.08282
SHDL	33.82335	35.58186	31.59035
SHDD	-12.38358	-12.59666	-14.02212
SPDL	28.77417	29.14766	28.27499
SPAL	52.09155	49.81068	52.67021
SDFPT	-32.02899	-33.38045	-29.94910
SDFPV	2.84213	2.66784	3.82468
SDFAN	-11.25096	-10.70128	-12.01646
SDFCD	36.22745	37.18388	35.81694
SDPTH	5.66489	7.21430	7.22136
SAFCD	96.28789	96.06682	94.18390
SMAxCD	-3.09521	-1.92577	-3.77663
SMINCD	-3.40272	-3.27335	-3.55577
CONSTANT	-5631.56250	-5709.84766	-5506.52734

VARIABLE	D	E	F	G	H
SPTAL	46.73357	45.34224	50.28116	44.87584	47.13049
SHDL	34.40082	33.65062	38.51878	33.74896	35.62016
SHDD	-12.16265	-12.43948	-11.81770	-14.13281	-14.93470
SPDL	28.91974	28.24757	27.61795	27.98395	29.66193
SPAL	51.10262	50.62512	49.91853	51.86581	49.10345
SDFPT	-33.40724	-31.81544	-36.34398	-31.43750	-32.80009
SDFPV	2.43589	3.23627	4.73521	4.60741	3.83589
SDFAN	-10.41694	-10.79062	-10.81750	-11.74489	-10.50931
SDFCD	36.81961	35.65433	36.66988	36.22061	37.57224
SDPTH	5.64779	6.23209	5.37802	7.19789	8.96522
SAFCD	96.88881	94.50584	97.81372	95.59657	94.89450
SMAxCD	-1.75959	-1.75475	2.74571	-1.42325	-1.45033
SMINCD	-2.46381	-3.29424	-0.53630	-2.31404	-3.19408
CONSTANT	-5694.58984	-5493.84766	-5903.92969	-5654.00000	-5755.45703

*Classification functions for 8 species of *Semionotus* based on 13 measurements entered as percentages of standard length. Variable names are listed in the left column. A through H are groups of individuals having similar shapes. New individuals can be classified as to group by calculating a classification function for each possible group as follows: the value of each variable for the unknown is multiplied by the corresponding coefficient of that variable within a group. These terms plus the constant term are summed for each group. The unknown is best identified as belonging to the group for which the value of the classification function is highest. Groups A through H correspond to species as follows: A) *S. kirschi*; B) *S. olseni*; C) *S. virginiae*; D) *S. thomsoni*; E) *S. euthenius*; F) *S. convalis*; G) *S. redfieldii*; H) *S. schaefferi*; Contents of Table 1 appear on the following page.

heavily influenced by the variables body depth (DPTH), head depth (HDD), and preanal length (PAL) (Table 2). Consistent with the dominance of depth on the first canonical variable is the dominance of depth variables entering early in the step function. The first variable entered was body depth (DPTH), and of the first five variables entered (DPTH, DFCD, HDD, DFPT, DFPV), four of them were principally depth variables.

Raw variables with the highest loadings on the second canonical variable, which accounts for an additional 25% of the total variance, are the distance between the pectoral and anal fins (PTAL), head length (HDL), the distance from the dorsal fin to the pectoral fins (DFPT), and the distance from the anal fin to the base of the axial lobe of the tail. They are essentially length variables that also fix the position of the ventral fins (pectoral and anal) along the horizontal axis. The position of pelvic fins is noticeably missing, but I took no measurements involving the pelvic fins other than their distance from the dorsal fin (DFPV), which is more a measure of depth than length.

Another 9% of the variance is picked up by the third canonical variable. It is

Table 2. Coefficients for canonical variables

VARIABLE	CANONICAL VARIABLES			
	1	2	3	
SPTAL	-0.17679	0.61952	0.10014	
SHDL	-0.19310	0.50173	0.05200	
SHDD	0.24335	0.24398	-0.21262	
SPDL	-0.05129	0.09259	0.37375	
SPAL	0.23484	-0.26709	-0.14851	
SDFPT	0.06313	-0.55499	-0.03212	
SDFPV	-0.14027	-0.15802	-0.24803	
SDFAN	-0.02822	0.20137	0.10263	
SDFCD	-0.10979	0.17374	0.32023	
SDPTH	-0.29671	-0.16414	0.31110	
SAFCD	0.10088	0.38182	0.06893	
SMAxcd	-0.17501	0.32838	-0.42435	
SMINCD	-0.03721	0.16048	-0.22393	
CONSTANT	12.26192	-32.99413	-24.47219	

VARIABLE	4	5	6	7
SPTAL	-0.09135	0.23710	0.30252	0.07436
SHDL	0.09457	0.69777	0.18633	0.12910
SHDD	-0.33821	0.11492	0.04353	0.35005
SPDL	0.02258	0.12794	-0.10875	-0.14116
SPAL	0.65597	-0.32376	0.07218	-0.18783
SDFPT	-0.06096	-0.14881	-0.08852	0.14477
SDFPV	0.25066	0.06182	0.10001	-0.22857
SDFAN	-0.32116	-0.01524	-0.40666	-0.08196
SDFCD	0.25962	-0.04291	0.11493	0.00321
SDPTH	0.01710	0.02836	0.34513	0.09176
SAFCD	0.72640	-0.06364	-0.09040	0.19968
SMAxcd	-0.12285	-0.01362	-0.21968	-0.09435
SMINCD	0.29633	-0.36191	-0.11832	-0.14335
CONSTANT	-69.63323	-6.74450	-15.93253	4.07923

VARIABLE #	1	2	3	4	5	6	7
EIGENVALUES	11.39046	4.63470	1.68808	0.70735	0.29358	0.12123	0.07896
CUM. PROP. TOTAL DISP.	0.60221	0.84725	0.93650	0.97389	0.98942	0.99583	1.00000
CANONICAL CORRELATIONS	0.95880	0.90693	0.79246	0.64366	0.47640	0.32883	0.27052

most heavily influenced by depth, particularly of the caudal peduncle. This variable may also reflect the position of the dorsal fin, specified on the longitudinal axis by its distance from the snout (PDL) and from the base of the axial lobe of the tail (DFCD).

Two length variables relating to anal fin position heavily dominate the fourth canonical variable, which accumulates another 3% of the total variance. The fifth canonical variable, which picks up another 2%, is essentially head length (HDL).

It has been quite obvious at every level of my analysis—from the specimens themselves, from the dominance of depth variables entered early in the discriminant analysis, and on the first canonical variable—that body depth is the most significant aspect of variation in the shape of these fishes. It is evident from the plot of the first and second canonical variable (Fig. 6) that the extreme groups, H, G, and A, are well separated by the first canonical variable (primarily a depth variable) alone, although there are other corroborating variables as well. The distinctions between groups B and E, E and D, and E and C are less clear and therefore merit the more detailed explanation provided in individual species descriptions. In order to help the reader visualize the actual differences in shape

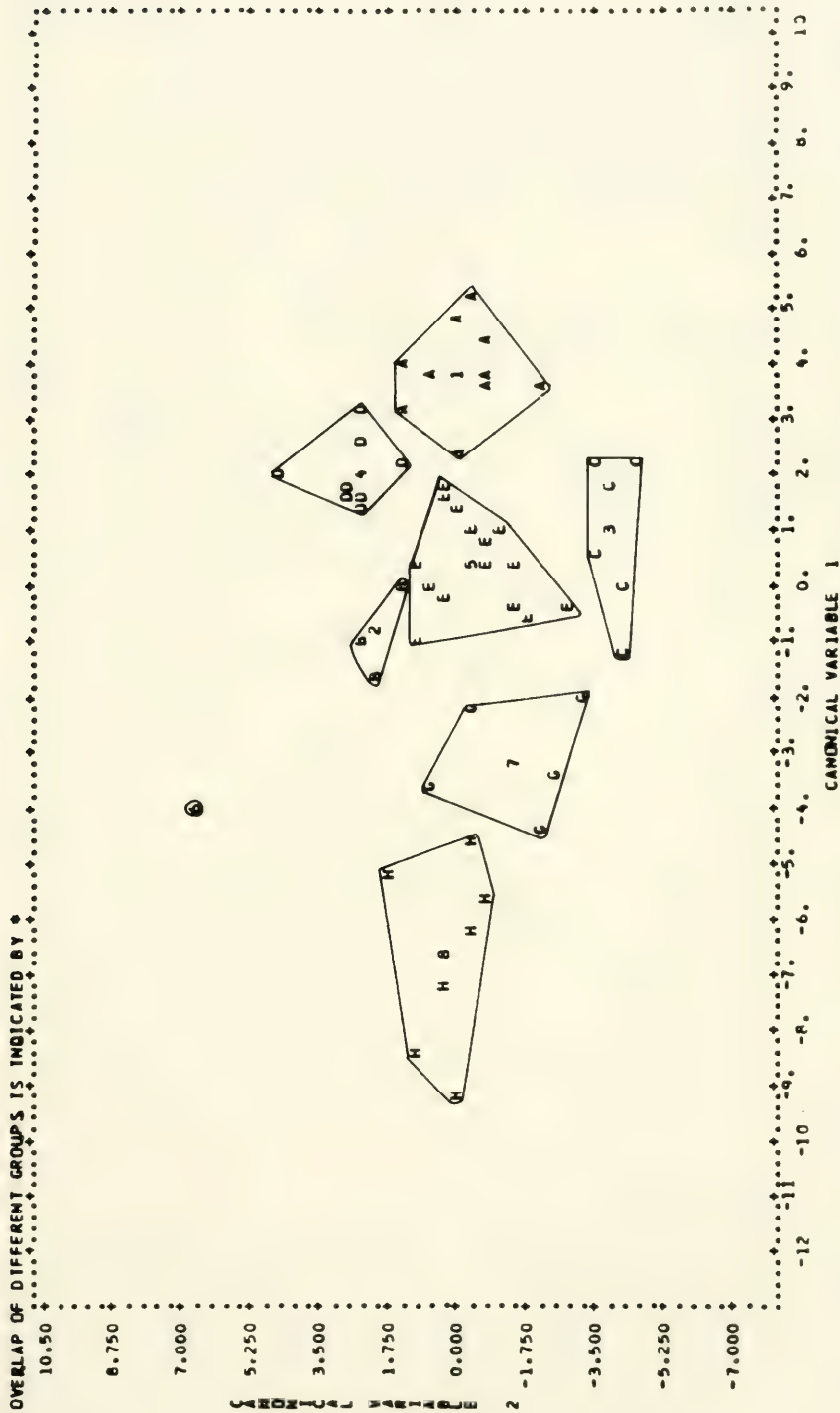


FIG. 6. Plot of canonical variables. Plot of the first canonical variable against the second canonical variable for complete individuals of *A. S. kirschi*; *B. S. olseni*; *C. S. virginiae*; *D. S. thomsoni*; *E. S. euthenius*; *F. S. convalis*; *G. S. redfieldii*; *H. S. schaefferi*. The first canonical variable is principally depth, while the second is a combination of lengths that specify the positions of fins along the longitudinal axis.

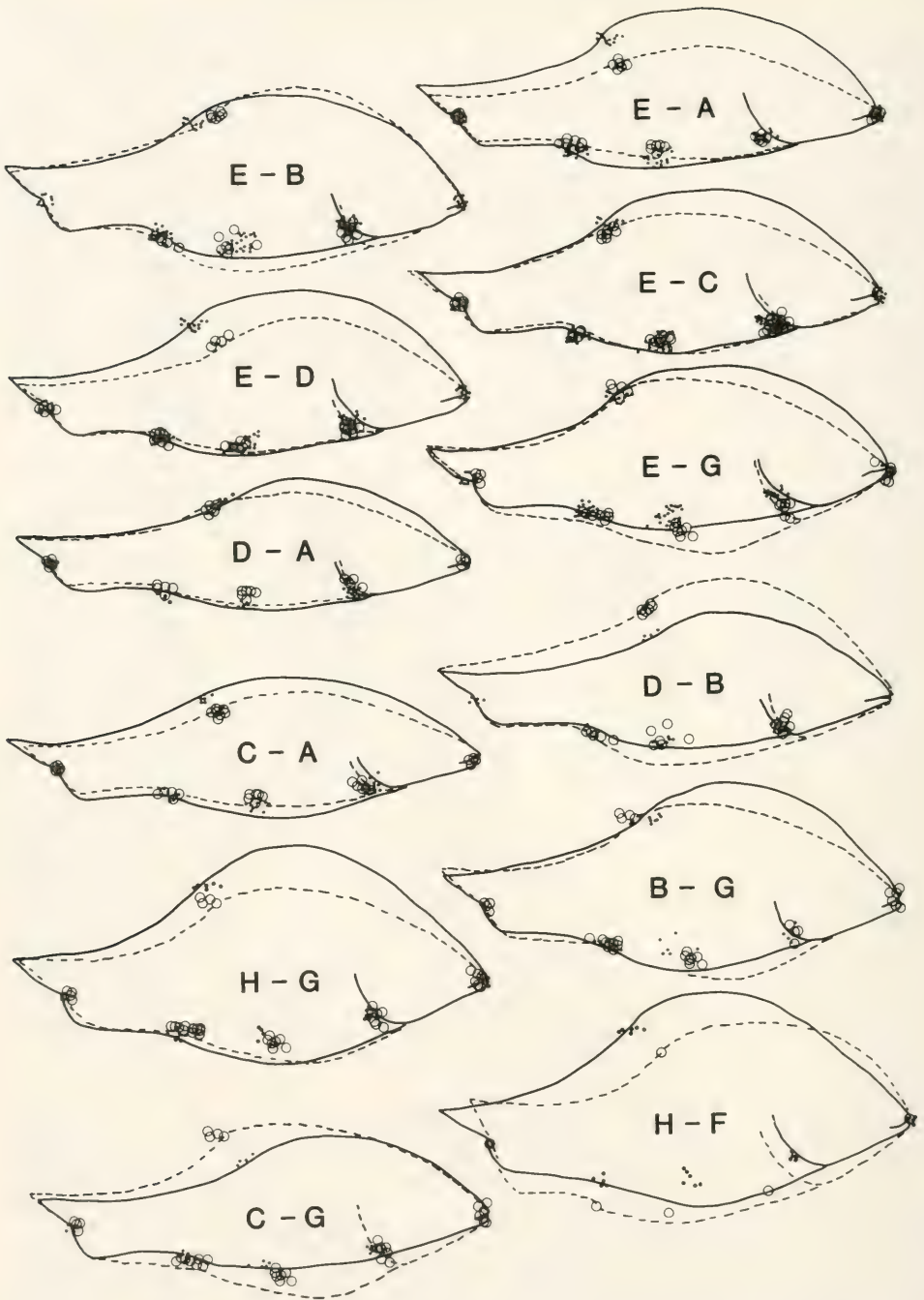


FIG. 7. Pairwise comparisons of Goodkin viewer tracings for eight species of *Semionotus*. Only comparisons of most similarly shaped species shown. A generalized outline for each species is given as a dotted or solid line. In each comparison, the symbol "o" is used for the scatter plot of positions that correspond to dotted outline; scatter plots of the symbol "." correspond to the solid outline. See Chapter 4 for a discussion of generating viewer groups. The subjects of each comparison are labeled by capital letters. The first letter of each pair in the figure corresponds to the solid outline, and the second letter to the dotted outline. For example, the comparison in the upper right-hand corner is between shape groups E and A. Group E is illustrated by the solid outline and "o" scatter plot. Group A is illustrated by the dotted outline and "." scatter plot. Groups A through H in these viewer comparisons correspond directly to the groups A through H used in the stepwise discriminant analysis (see Tables 1, 2, 3; Fig. 6). Each group also corresponds to the following species described herein: A, *S. kirschi*; B, *S. olseni*; C, *S. virginiae*; D, *S. thomsoni*; E, *S. euthenius*; F, *S. convalis*; G, *S. redfieldii*; H, *S. schaefferi*.

represented by this plot of canonical variables, I have superimposed morphotype-variability plots for the most similar-shaped pairs of groups (Fig. 7).

The table of canonical variables evaluated at group means (Table 3) gives at least a suggestion of the raw variables contributing most to the separation of groups. However, for operational taxonomy it is most useful to identify specific raw variables that will separate pairs of species, and it is customary to give regression equations for these variables as a function of standard length (SL). For each species described below, summary statistics and regression equations using the least squares method (Statistical Analysis System or SAS; Helwig and Council 1979) are included in the diagnoses of individual species.

Table 3. Canonical variables evaluated at group means

Group	1	2	3	4	5	6	7
A	3.79112	-0.36169	0.28118	0.67223	0.53322	-0.00612	-0.02867
B	-1.02602	1.88965	1.18823	-0.25776	-0.03810	0.88886	0.51158
C	0.62638	-3.82284	0.23234	-0.00222	-0.64458	0.38541	-0.29186
D	2.03933	2.54510	0.75193	0.14238	-0.66667	-0.28246	-0.05704
E	0.14956	-0.20950	-0.79674	-1.11402	0.12818	-0.11962	0.04652
F	-3.84094	6.82925	-5.14688	1.05456	0.21393	0.96448	-0.92937
G	-3.41671	-1.34862	-1.81941	1.36445	-0.31142	-0.24368	0.41590
H	-6.96589	0.06298	1.48888	0.13879	0.34007	-0.15407	-0.18622

6. SYSTEMATIC DESCRIPTIONS

*SEMIONOTUS*Genus *Semionotus* Agassiz 1832

Type species. *S. leptocephalus* Agassiz (1832 [name]; 1836: [description]; 1834: Tab. 26 [figure])

Paleothrissum (in part) Hitchcock, 1823

Eurynotes (in part) Agassiz 1835

Paleoniscus (in part) Redfield, W. C. 1841

Ischypterus Egerton, 1850 (no type species designated)

Eurynotes Emmons, 1860

Ischypterus Newberry, 1888 (no type species designated)

Semionotus Woodward, 1895 (type species *Semionotus bergeri*); Woodward (1895) and most others before him commonly used *S. bergeri* as the type species. The reasons for this irregularity are discussed elsewhere (McCune 1986). A petition has been submitted to the International Commission on Zoological Nomenclature to designate *S. bergeri* as the type species and to annul Agassiz's designation of *S. leptocephalus* (McCune 1985)

Etymology. *Semionotus*, meaning "signal back," refers to the modified scales along the dorsal midline

Age. Late Triassic, Early Jurassic

Revised diagnosis (from McCune 1986). Halecostome fishes that share the following synapomorphies with *Macrosemius* and *Lepisosteus*: gular and intercalar lost; epiotic with large posteriorly directed process; premaxilla with long nasal processes; only arch of mesocoracoid ossified in shoulder girdle; first infraorbital subdivided; ethmoidal ossification reduced to splint (Olsen 1984c). *Semionotus* lacks the synapomorphies that define the macrosemiids (Olsen 1984c) and lepisosteids (Wiley 1976) and shares with *Lepidotes* a series of simple, convex scales with moderate to well-developed, posteriorly directed spines along the dorsal midline between the extrascapulars and the origin of the dorsal fin. *Semionotus* has a single anamestic suborbital, whereas *Lepidotes* has two or more suborbitals (Fig. 8). A single anamestic suborbital has been interpreted as a derived trait among primitive actinopterygians (Schaeffer and Dunkle 1950; Patterson 1973; Wiley 1976); if this is correct, then *Semionotus* is monophyletic and includes all semionotids from the Newark Supergroup and a number of European semionotids (McCune 1986).

Description. The morphology of *Semionotus* is being described based on excellent material from the Newark Supergroup (Olsen and McCune ms). Most of this information need not be reiterated here. However, the morphology of semionotid dorsal ridge scales and my interpretation of them figure prominently in the text that follows and thus will be discussed below.

Both *Semionotus* and its sister genus *Lepidotes* have a row of modified scales along the dorsal midline between the nape and the origin of the dorsal fin. In *Lepidotes* and most species of *Semionotus* found outside Newark deposits including the type species, *S. bergeri*, these scales are dorsally convex and entirely covered with ganoine. The anterior scales have short, posteriorly directed spines and are almost triangular in shape; the spines lengthen posteriorly, often with a slight constriction between the base of the spine and the base of the scale. I refer to

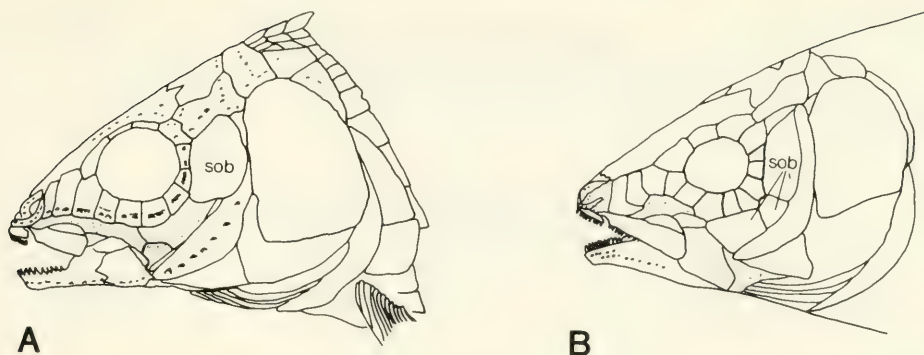


FIG. 8. Comparison of the skulls of *Semionotus* and *Lepidotes*. A, *Semionotus* after Olsen and McCune (ms); B, *Lepidotes* after Wenz (1967). Stippled regions are medial to the dermal skull. Note that much of the palate is visible in *Semionotus* (stippled area), whereas the palate is almost completely covered by extra suborbitals in *Lepidotes*. Reproduced from *Palaeontology* (1986), 29(2), p. 213–233, A revision of *Semionotus* (Pisces: Semionotidae) from the Triassic and Jurassic of Europe, by A. R. McCune.

these as “simple scales” (Fig. 9A) following Olsen and others (1982) and the species that have them as an informal species group, the *S. bergeri* group.

In addition to simple scales, a variety of other forms of dorsal ridge scales are found on Newark semionotids. In Towaco cycle P4, there are six other distinct types.

The modified simple-scale type is only a slight variant of the simple-scale type (Fig. 9B). Modified simple scales are distinguished from simple scales by lateral undercutting of the spine so that in dorsal view the spine appears to be supported by a wider scale base. The spine (unstippled in Fig. 9B) is covered by ganoine while the surrounding base is naked bone. Both the distribution of ganoine on the dorsal surface of the scale and the undercutting lateral to the spine occur in varying degrees within some species. In *Semionotus minor* (McCune 1986), the distribution of ganoine is particularly easy to see by its color and texture relative to bone. In this species, the extremes of variation range from short-spined scales covered completely with ganoine to longer-spined scales with only the central axis of the spine covered by ganoine (Fig. 10A). At least in some *Lepidotes toombsi* (probably *Semionotus*; see McCune 1986) and *Lepidotes mawsoni*, the ganoine does not cover the entire dorsal surface of the bone (Fig. 10). However, for these two species I have not been able to assess the range of intraspecific variability. Several species of *Semionotus* from P4 show undercutting lateral to the spine at least in a few individuals, but, as the best specimens are negatively prepared, it is harder (though possible by differences in texture) to see the distribution of ganoine on the scale.

Modified simple scales are intermediate between simple scales and thin-spined scales. Thin-spined scales (Fig. 9D) have very long, slender spines that cut away from the scale base more abruptly than in modified simple scales. Distally, the spine is supported by a flange of bone barely wider than or the same width as the spine itself. Only the dorsal surface of the spine is covered by ganoine.

In contrast to other types of dorsal ridge scales, small scales (Fig. 9C) are about the same size as or smaller than flank scales. The spines of these scales are short and distinct from the scale base (compare with the short-spined anterior scales of the simple-scale type).

Robust and globular dorsal ridge scales (Fig. 9E, F) are the most distinctive of any semionotid dorsal ridge scales for the size and shape of their anterior scales. In the robust type (Fig. 9F), along the anterior-posterior axis, the spines are

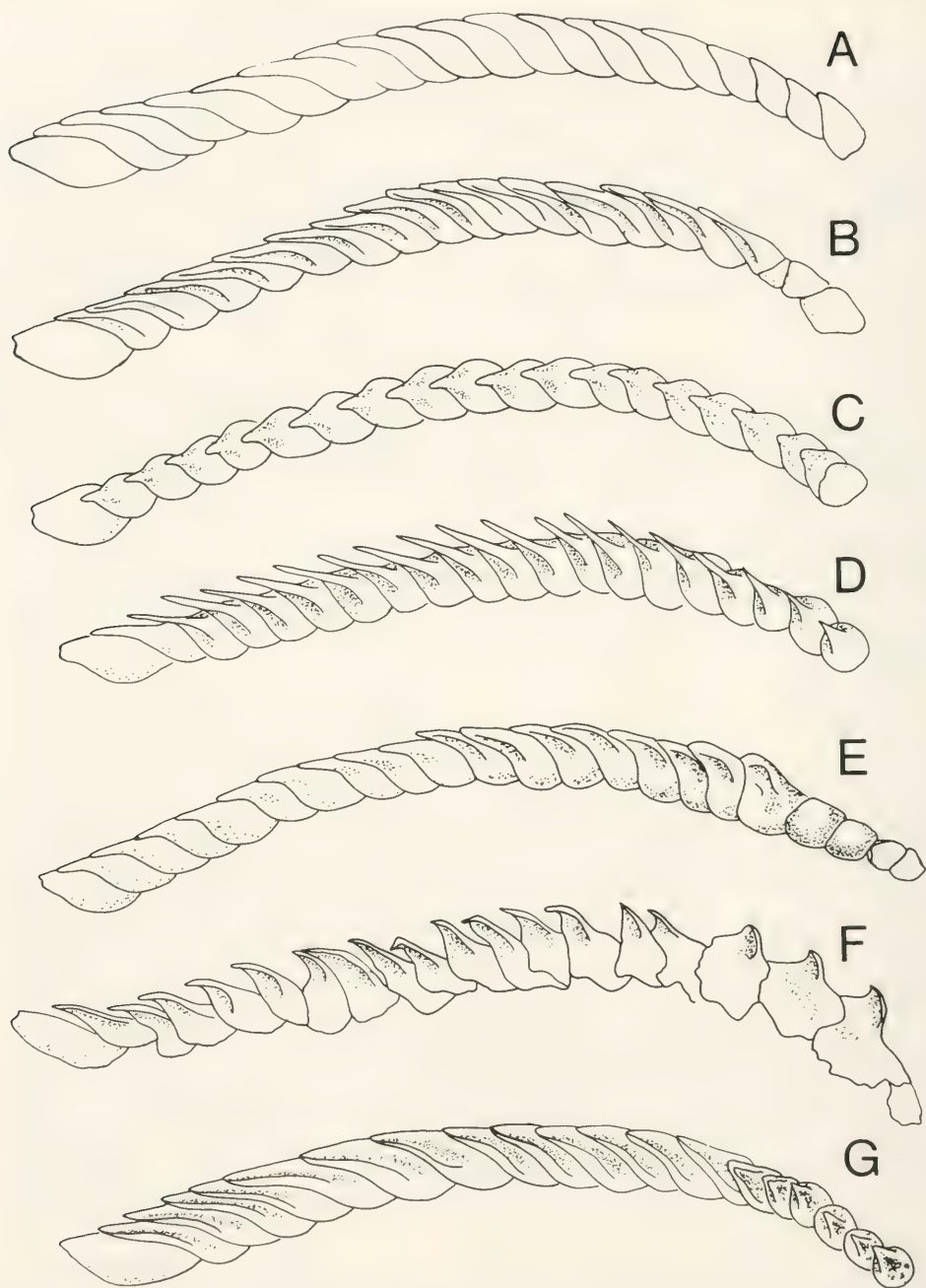


FIG. 9. Morphological diversity of the dorsal ridge scales of semionotid fishes from cycle P4, Towaco Formation, Newark Basin. Scales rim the dorsal midline between the nape and the origin of the dorsal fin. The anterior direction is toward the right in each series pictured; spines are directed posteriorly. A, simple scales, corresponding to those of the simple-scale group (Olsen and others 1982); B, modified simple scales; C, small scales, corresponding to those of the small-scale group (Olsen and others 1982); D, thin-spined scales, corresponding to those of the "*S. micropterus* group" (Olsen and others, 1982); E, globular scales; F, robust scales, corresponding to those of the *S. tenuiceps* group (Olsen and others 1982); G, concave scales, corresponding to those of the *S. elegans* group (Olsen and others 1982). Reproduced from McCune and others, 1984, Semionotid fishes from the Mesozoic great lakes of North America, p. 27–44. In A. A. Echelle and I. Kornfeld [eds.] Evolution of fish species flocks. University of Maine Press, Orono.

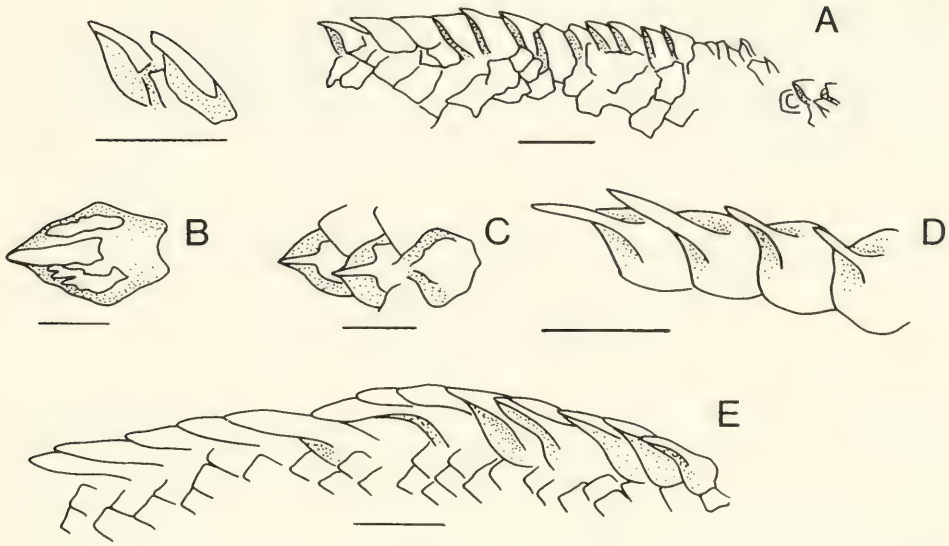


FIG. 10. Distribution of ganoine on the dorsal surface of the dorsal ridge scales of various semionotids. A, *S. minor* BMNH 41157 (left), BMNH 36081 (right); B, *Lepidotes mawsoni* BMNH P.10372; C, *L. toombsi* BMNH 25180; D, *Semionotus* sp. YPM 8604, from North Guilford, Connecticut; E, *S. anosteus* YPM 8844. Scale = 5 mm.

dorsally convex. In lateral view, they are undercut slightly beneath the spine and the bases expand ventrally. The first two scales are small and spineless, but beginning with about the third scale, there are six to eight very large angular scales. These scales are broad at the base in an anterior-posterior direction and about two to three times the width of a normal flank scale. The spines are small relative to the scale base, and instead of pointing in a posterior direction, they point first dorsally and then posteriorly. The spines do not extend or extend only slightly beyond the scale base. On anterior scales, ganoine covers only the spine and the central portion of the scale base.

Globular scales (Fig. 9E) are more moderately developed than robust scales. The former are smaller than robust scales, and their bases tend to be more bulbous than angular. Scale enlargement begins more posteriorly in globular scales than in robust scales. In both types, the posterior scales are simple, convex, and have well-developed spines, though in at least one individual (YPM 8932) the posterior spines have short, distinct spines similar to those of the small-scale type.

The most common dorsal ridge scale morphology among semionotids is the simple-scale type (Fig. 9A). Simple scales are found on semionotids from several Newark localities (Olsen and others 1982), in all European species of *Semionotus*, *Lepidotes laevis* (MHHP 1905-17), *L. mantelli* (BMNH P.6933), and *L. toombsi* (BMNH P.25180). Although a complete series (nape to dorsal fin) of dorsal scutes or scales is rare within the Actinopterygii, a number of paleoniscids and elonichthyids have a partial series of modified dorsal scales that closely resemble simple scales in form (Orlov 1967). Thus, I interpret simple scales as primitive and the other types of dorsal ridge scales as derived. The relative polarities of the other dorsal ridge scale morphologies will be discussed in more detail in Chapter 8, but it is relevant here to note that certain of these other scale types may define monophyletic groups; however, because species having simple scales share no synapomorphies not also shared by forms with more derived dorsal ridge scales, these monophyletic subgroups recognizable by dorsal ridge scale morphology cannot be named as genera without rendering *Semionotus* paraphyletic. Thus, I

will leave these subgeneric complexes as informal species groups. Those species having simple dorsal ridge scales (Fig. 9A) I will refer to as the *S. bergeri* species group; those with robust scales (Fig. 9F) the *S. tenuiceps* group; and those with concave dorsal ridge scales (Fig. 9G) the *S. elegans* group. I will argue that the latter two groups are monophyletic.

THE *SEMIONOTUS BERGERI* GROUP

Semionotus kirschi, new species

Figs. 5, 6, 7, 11A, 11B, 40; Tables 1, 2, 3, 4, 5, 6, 32

Diagnosis. *S. kirschi* is distinguished from all other species of *Semionotus* having simple dorsal ridge scales by its very slender body and relatively long head. Its slender body form is reflected quantitatively in the measurements and regression equations summarized in Tables 4 and 5. For identification, I have provided an outline drawing of this species (Figs. 5, 11A) as well as the classification function in Table 1. Although *S. kirschi* is most similar to *Semionotus virginiae* and *Semionotus thomsoni* (described below; see Figs. 6, 7), it can be readily distinguished using a number of measurements. Relative to standard length, DFPV, MINCD, PTAL, DFPT, MAXCD, and MINCD are all less in *S. kirschi* than in *S. virginiae*. Similarly, the values of HDD, DFCD, MINCD, DFAN, MAXCD, and DPTH, all relative to standard length, are less for *S. kirschi* than for *S. thomsoni*.

Holotype. YPM 8718 (P4-2655) complete fish, mechanically prepared (see Fig. 40)

Paratypes. YPM specimens 6501, 6519, 6524, 6585, 8709, 8712, 8713, 8714, 8715, 8716, 8717, 8719, 8720, 8722, 8724, 8725, 8727, 8729, 8884, 8887, 8895, 8909

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. For J. A. W. Kirsch, in recognition of his contribution to systematic biology as both teacher and scientist

Description. The dorsal ridge scales of *S. kirschi* are simple and nearly triangular. In most specimens, the anterior scales are either not well preserved or not visible on their dorsal surface, but the holotype shows these scales well. The first three scales are very round at the base, with a very short narrow spine (Fig. 11). Posterior scales have longer spines that taper smoothly from the base to the tip. The last scale in the series is a large oval plate that abuts the first (unpaired) fulcrum on the leading edge of the dorsal fin. The total number of scales in the dorsal series, including the predorsal scale, is about 19.

This species is the most slender and streamlined of the *S. bergeri* group. The head is larger relative to other slender *Semionotus* such as *S. bergeri* and *S. virginiae*, and the slope of its forehead with respect to horizontal is about 15–25°. Overall body form is most clearly seen by comparison of outline drawings (Fig. 11A) of *Semionotus* with simple scales from the Yale P4 excavation. By visual inspection or by superimposing a tracing of *S. kirschi* on outlines of the other species (all at

A



B

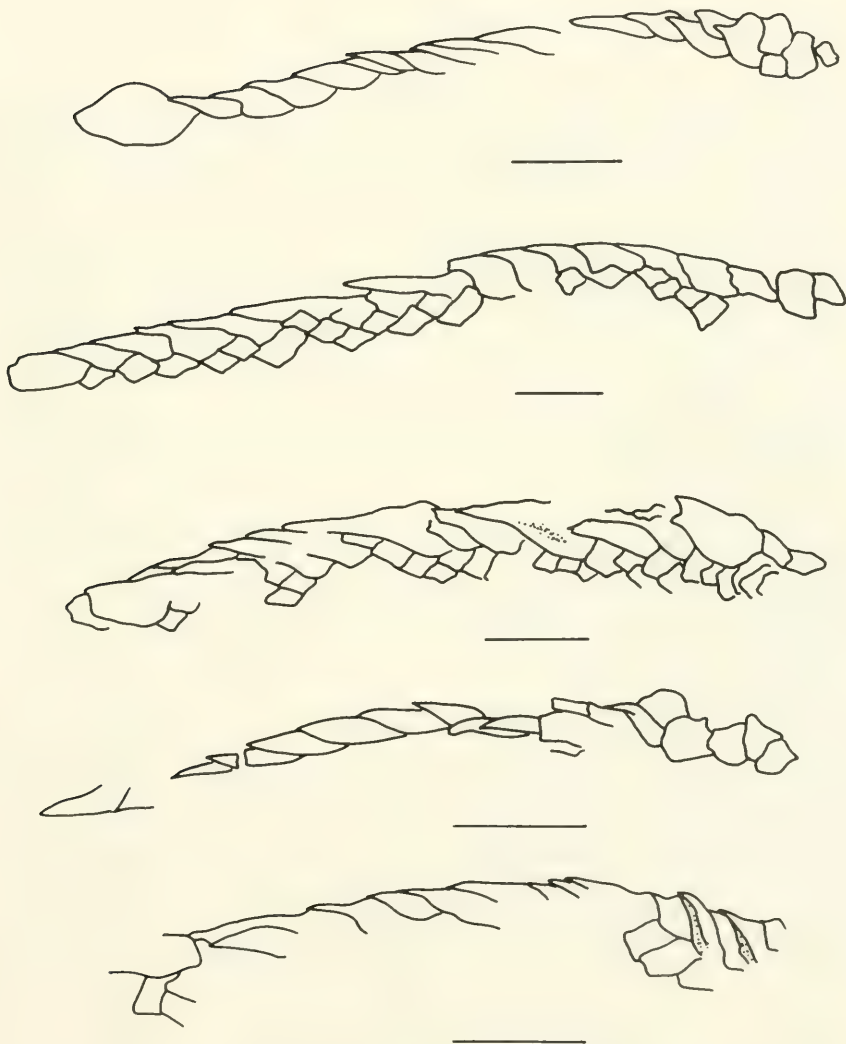


FIG. 11. *S. kirschi*. A, outline of body traced from YPM 6585, fins based on YPM 8895 (caudal), 8722 and 8719 (pelvics, pectorals, and dorsal); B, camera lucida drawings of dorsal ridge scales of YPM specimens 8718, 8725, 8719, 8722, 8724. Scale = 5 mm.

Table 4. Summary of morphometric data for *Semionotus kirschi*. MAXCD expressed as % AFCD. All other variables but SL expressed as % SL.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
SL	13	10.36	1.36	8.30	12.60
DPTH	13	27.62	1.51	25.00	31.33
HDL	13	30.89	1.40	27.96	32.74
PDL	12	64.04	1.86	61.90	67.47
DFPV	12	23.94	2.45	20.69	29.03
DFAN	12	23.33	1.49	20.18	25.00
DFCD	13	38.98	2.33	35.78	42.86
AFCD	11	28.03	2.32	23.81	31.18
HDD	13	21.16	1.86	17.20	23.81
DFCD	13	38.98	2.33	35.78	42.86
MAXCD	12	12.98	1.00	11.11	14.46
MINCD	12	11.11	0.68	9.57	12.05
PTAL	10	45.41	1.50	42.86	47.87
DFPT	11	40.28	2.58	37.93	46.24
MAXCD	14	45.73	3.51	41.38	52.17

the same standard length), one can easily see that *S. kirschi* is more slender than any of the species in this group (Figs. 6, 7). The shape of *S. kirschi* can be described quantitatively by the set of individual linear measurements summarized in Tables 4 and 5 or by a classification function of the same measurements in linear combination (Table 1).

There are 33–39 (mean = 36) lateral line scales. The pelvic fin originates between the 8th and 11th scale row, the anal fin between rows 18–22, and the dorsal fin between rows 20–24, but always one or more scale rows behind the anal fin. Rarely, there are intercalated scale rows dorsal to the lateral line and anterior to the dorsal fin. The scales are largest in the anterior flank region and around the lateral line. They decrease in size both caudally and anterodorsally. The scales along the dorsal and ventral midline of the caudal peduncle are enlarged. From the lateral line, there are 7–8 scales to the dorsal fin and about 8 to the origin of the anal fin.

The dorsal and anal fins are fringed with 6–8 fulcra; the first three are basal fulcra, and the bases of the next two lie against the unsegmented portion of the first lepidotrichium. There are 9–14 dorsal and 8–10 anal lepidotrichia. The pectoral and pelvic fins are fringed by at least 5–7 fulcra. Pelvic lepidotrichia number 3–5 and pectoral lepidotrichia number 11–16. Meristic data are summarized in Table 6.

The posterior margin of the fins is difficult to see because the segmented portions of the lepidotrichia fade distally. However, in all fins the tips of the lepidotrichia extend beyond the tip of the last fin fulcrum. The posterior margin of the dorsal fin reaches at least to the region where the scales along the dorsal midline of the caudal peduncle begin to enlarge, or about halfway between the dorsal and caudal fins (YPM 8719). The caudal fin is weakly emarginate (Fig. 11A; YPM 8719). The pelvic fins reach as far back as the preanal scale when appressed to the body. The pectoral fins stop just short of the origins of the pelvics (YPM 8722, YPM 8719).

Semionotus olseni, new species

Figs. 5, 6, 7, 12A, 12B, 40; Tables 1, 2, 3, 7, 8, 9, 32

Diagnosis. This species is among the most deep-bodied forms of the *S. bergeri* group. It differs from *S. bergeri*, *S. kirschi*, *S. virginiae*, and *S. thomsoni* (the latter two described below) by the depth of its body relative to standard length and by

Table 5. Parameter values of the regressions and correlation coefficients for *Semionotus kirschi*. For MAXCD, the independent variable is AFCD; for all other dependent variables, the independent variable is SL.

Variable	N	Y intercept	Slope	Correlation coefficient
DPTH	13	0.42	0.23	0.86
HDL	13	-0.42	0.35	0.93
PDL	12	0.56	-0.59	0.96
PAL	12	-1.09	0.84	0.97
DFPV	12	0.68	0.17	0.54
DFAN	12	-0.48	0.28	0.89
DFCD	13	-0.49	0.44	0.86
AFCD	11	0.86	0.20	0.64
HDD	13	0.46	0.17	0.66
MAXCD	12	0.38	0.09	0.66
MINCD	12	0.04	0.11	0.84
PTAL	10	-0.36	0.49	0.96
DFPT	11	0.86	0.32	0.76
MAXCD	14	0.32	0.34	0.61

the suite of correlated measurements that also reflect body depth to some degree. It is only slightly deeper bodied than the two most similarly shaped species, *Semionotus kapffi* and *Semionotus euthenius*. (See the plot of the first two canonical variables in Fig. 6 and the outline drawings in Figs. 5 and 12.) It differs from these two species in the following measurements relative to standard length: DPTH, DFAN, MINCD, and HDD. For identification, I provide an outline drawing of *S. olseni* (Fig. 12A) as well as a classification function (Table 1) and regression equations (Table 8).

Holotype. YPM 6538; complete fish, no counterpart, negatively prepared (see Fig. 40)

Paratypes. YPM specimens 6538, 8679, 8730, 8733, 8734, 8805, 8852, 8882, 8891, 8907

Table 6. Summary of meristic data for *Semionotus kirschi*

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
VDSC	3	7.7	0.6	7.0	8.0
VVSC	3	8.0	0.0	8.0	8.0
PLVSC	15	9.4	0.7	8.0	11.0
ANFSC	16	19.2	1.2	18.0	22.0
DFSC	17	21.5	1.2	20.0	24.0
CDSC	15	35.7	1.5	33.0	39.0
AXSC	11	8.7	0.8	8.0	10.0
PCTR	6	14.0	1.9	11.0	16.0
PLVR	7	3.6	0.8	3.0	5.0
ANFR	7	8.4	0.8	8.0	10.0
DFR	11	11.6	2.0	9.0	14.0
CDDR	5	8.2	1.1	7.0	9.0
CDVR	10	8.0	0.0	8.0	8.0
DFF1	11	3.3	0.5	3.0	4.0
DFF2	9	4.7	0.5	4.0	5.0
DFF3	11	7.2	0.8	6.0	8.0
AFF1	6	3.0	0.0	3.0	3.0
AFF2	6	5.2	0.4	5.0	6.0
AFF3	11	6.4	0.5	6.0	7.0
PCTF	2	6.0	1.4	5.0	7.0
PLVF	6	6.2	0.4	6.0	7.0
CDF	1	7.0	-	7.0	7.0
CVF	4	6.5	0.6	6.0	7.0

Table 7. Summary of morphometric data for *Semionotus olsen*. MAXCD expressed as % AFCD. All other variables but SL expressed as % SL.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
SL	10	8.39	1.00	7.00	9.80
DPTH	9	41.44	2.16	38.36	44.19
HDL	10	31.04	1.70	29.17	33.80
PDL	10	64.28	2.71	60.42	69.32
DFPV	5	31.91	3.34	29.07	36.62
DFAN	8	32.73	1.45	30.00	34.29
DFCD	10	45.46	1.88	42.05	48.57
AFCD	8	28.69	1.76	25.93	31.40
HDD	9	30.01	2.60	25.51	33.80
DFCD	10	45.46	1.88	42.05	48.57
MAXCD	8	17.63	0.94	16.28	18.75
MINCD	9	15.62	1.16	14.29	17.44
PTAL	8	44.47	2.67	39.53	46.58
DFPT	9	43.29	2.61	39.80	48.86
MAXCD	7	61.64	2.98	58.33	66.67

Type locality. In the same section (cycle) as the 1979–80 Yale P4 excavation in Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Referred specimens. 8731, 8732, 8922

Etymology. For P. E. Olsen, in honor of his wide-ranging contributions to the geology, paleontology, and paleolimnology of the Newark Supergroup

Description. The dorsal ridge scales of *S. olsen* are convex and almost triangular in dorsal view. The spines increase in length posteriorly, but along the entire series they taper smoothly from the base to the tip. The last scale in the series is a large oval plate that abuts the first fulcrum on the leading edge of the dorsal fin. The total number of scales in the dorsal series, including the predorsal scale, is about 20. Although these dorsal ridge scales share their basic form with those

Table 8. Parameter values of the regressions and correlation coefficients for *Semionotus olsen*. For MAXCD, the independent variable is AFCD; for all other dependent variables, the independent variable is SL.

Variable	N	Y intercept	Slope	Correlation coefficient
DPTH	9	-0.26	0.44	0.83
HDL	10	0.36	0.27	0.80
PDL	10	0.38	0.60	0.87
DFPV	7	-0.46	0.77	0.79
DFAN	5	1.72	0.11	0.57
DFCD	8	0.47	0.27	0.86
AFCD	10	0.24	0.42	0.89
HDD	8	0.08	0.28	0.76
DFCD	9	0.85	0.20	0.45
MAXCD	8	0.06	0.17	0.71
MINCD	9	0.00	0.16	0.67
PTAL	8	-0.06	0.45	0.84
DFPT	9	0.22	0.41	0.77
MAXCD*	7	0.25	0.52	0.86

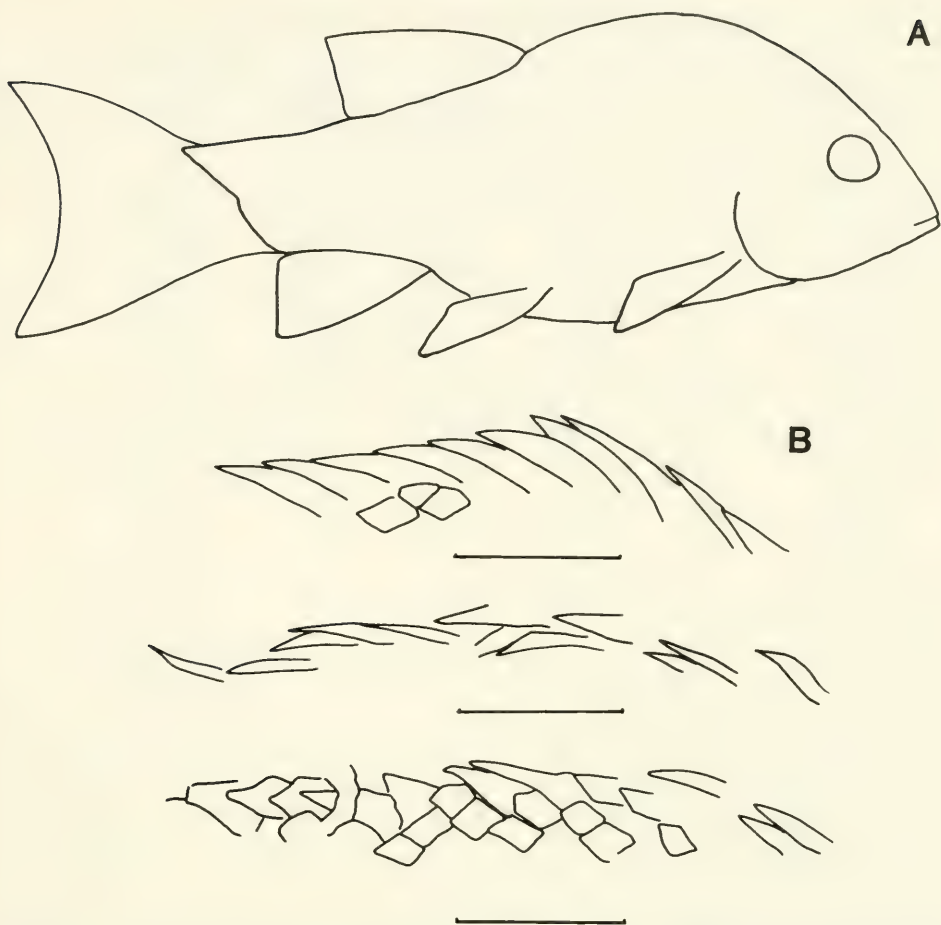


FIG. 12. *S. olseni*. A, outline of body form, Lazy Lucy tracing of YPM 6538; B, camera lucida drawings of dorsal ridge scales in YPM specimens 6538, 8907, 8891. Scale = 5 mm.

of other *Semionotus* bearing simple scales, the scales in this species are almost knife-like, and larger than in other species, such as *S. kirschi* (Fig. 12B).

S. olseni is relatively deep bodied, with a deep head and caudal peduncle. The fins are placed approximately as in other semionotids, the caudal peduncle is moderately deep, and the slope of the forehead with respect to horizontal is about 50–60°. The classification function (Table 1) describes quantitatively the shape of this species relative to all others, but because using the classification function for identification can be unwieldy, I also provide an outline drawing of this species (Fig. 12A) and a summary of individual measurements (Tables 7, 8).

There are 33–37 (mean = 35) lateral line scales. The pelvic fin originates between the 8th and 10th vertical scale row, the anal fin between rows 17–19, and the dorsal fin between rows 18–22, but always one or more scale rows behind the anal fin. Meristic data are summarized in Table 9.

No specimens that have intercalated scale rows dorsal to the lateral line and anterior to the dorsal fin are known. Flank scales are largest in the anterior region near the lateral line. They decrease in size both caudally and anterodorsally. The scales along the dorsal and ventral midline of the caudal peduncle are enlarged. From the lateral line, there are 9–11 scales to the dorsal fin and about 9 to the origin of the anal fin.

Table 9. Summary of meristic data for *Semionotus olsen*

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
VDSC	2	10.0	1.4	9.0	11.0
VVSC	1	9.0	—	9.0	9.0
PLVSC	6	8.7	0.8	8.0	10.0
ANFSC	8	18.4	0.7	17.0	19.0
DFSC	10	20.5	1.3	18.0	22.0
CDSC	8	34.6	1.3	33.0	37.0
AXSC	3	8.7	1.2	8.0	10.0
PCTR	1	15.0	—	15.0	15.0
PLVR	1	5.0	—	5.0	5.0
ANFR	1	10.0	—	10.0	10.0
DFR	1	12.0	—	12.0	12.0
CDDR	0	—	—	—	—
CDVR	1	8.0	0.0	8.0	8.0
DFF1	3	3.3	0.6	3.0	4.0
DFF2	2	5.0	0.0	5.0	5.0
DFF3	2	7.5	0.7	7.0	8.0
AFF1	2	3.0	0.0	3.0	3.0
AFF2	0	—	—	—	—
AFF3	1	8.0	—	8.0	8.0
PCTF	1	10.0	—	10.0	10.0
PLVF	4	5.8	1.5	5.0	8.0
CDF	0	—	—	—	—
CVF	1	8.0	—	8.0	8-0

The dorsal fin is fringed with 6–8 fulcra; the first three are basal fulcra, and the base of the next one lies against the unsegmented portion of the first lepidotrichium. The anal fin fulcra are not well preserved in any known specimen. In single specimens showing the dorsal and anal lepidotrichia, there were 10 and 12 rays, respectively. The pectoral and pelvic fins are fringed by at least 10 and 5–8 fulcra, respectively. The number of pelvic fulcra is not unusual for *Semionotus*, but the number of preserved pectoral fulcra is unusually high relative to the 5–7 in other species. Whether this is a significant difference can only be determined if more specimens of this species become available. Again based on single specimens, there are 5 and 15 pelvic and pectoral lepidotrichia, respectively.

The posterior extent of fins is difficult to determine because the segmented portions of the lepidotrichia taper distally. However, in all fins the tips of the lepidotrichia extend beyond the tip of the last fin fulcrum. The posterior margin of the dorsal fin reaches at least to the region where the scales along the dorsal midline of the caudal peduncle begin to enlarge, or about halfway between the dorsal and caudal fins. The caudal fin is weakly emarginate (Fig. 12A). The anal fin reaches back as far as the beginning of the caudal fin (YPM 8735). When appressed to the body, the posterior tips of the pectoral fins almost touch the origin of the pelvics (YPM 6538) and the pelvic fins reach almost to the anal fin (YPM 8805).

Semionotus virginiae, new species

Figs. 5, 6, 7, 13A, 13B, 40; Tables 1, 2, 3, 10, 11, 12, 32

Diagnosis. This species is distinguished from all other species of *Semionotus* with simple scales except *S. kirschi* by its slender body form. It differs from *S. kirschi* by being slightly deeper bodied, a state reflected in the greater value of the measurements DFPV, MINCD, DFPT, MAXCD, and DPTH, all relative to standard length. The tail of this species appears to be more deeply forked than in all other species of *Semionotus* (Fig. 13) except *S. thomsoni*. For identification,

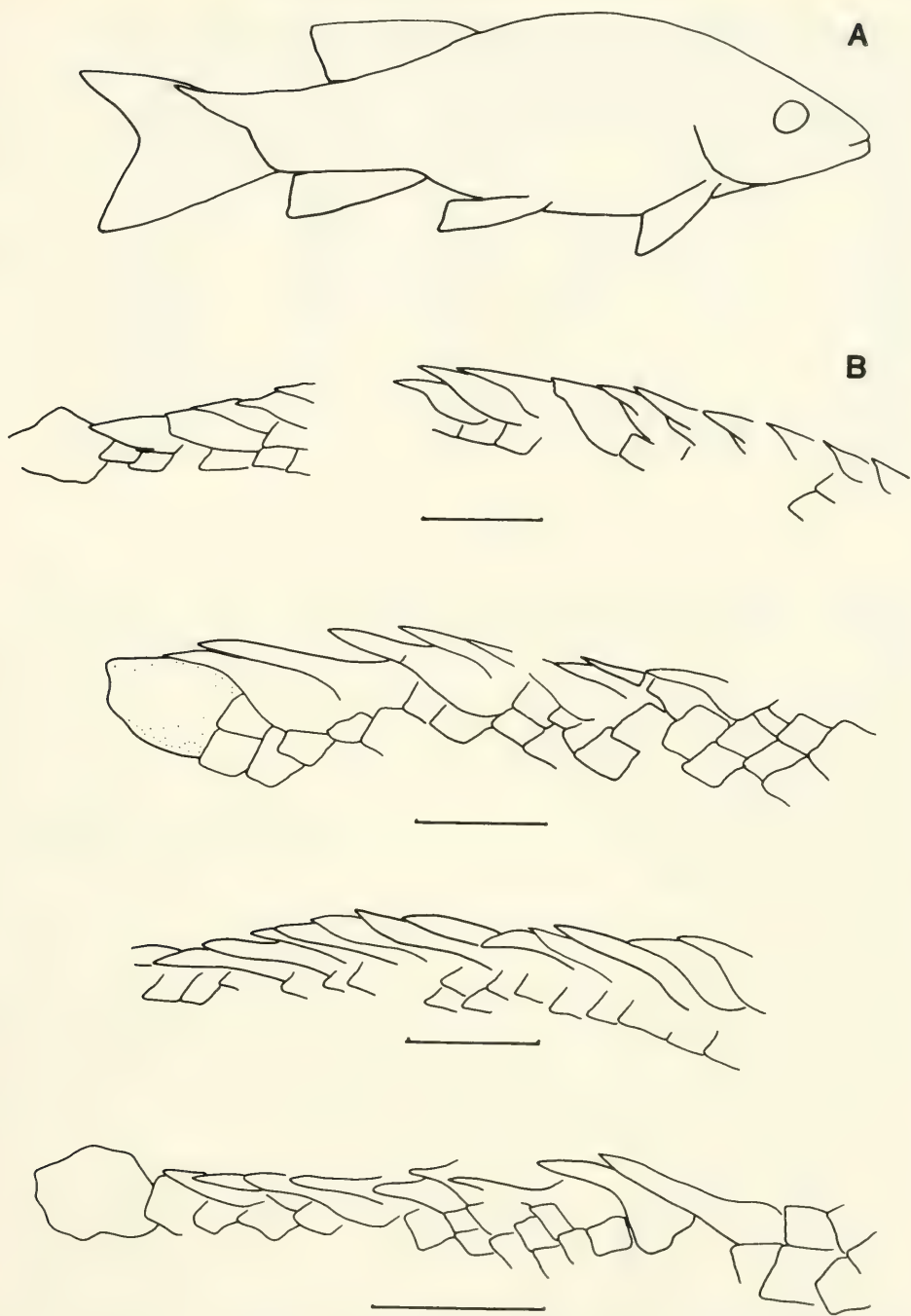


FIG. 13. *S. virginiae*. A, outline of body form traced from YPM 8740, fins based on YPM specimens 8738, 8864, 8741, and 8736; B, dorsal ridge scales of YPM specimens 8741, 8740, 8881, 8869. Scale = 5 mm.

an outline drawing of this species (Figs. 5, 7, 13A), a classification function (Table 1), morphometric data (Tables 10, 11; Fig. 6), and meristic data (Table 12) are provided.

Holotype. YPM 8740 (P4-716) complete fish, part and counterpart, negatively prepared (Fig. 40)

Table 10. Summary of morphometric data for *Semionotus virginiae*. MAXCD expressed as %AFCD. All other variables but SL expressed as % SL.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
SL	10	9.79	1.07	8.30	12.00
DPTH	9	34.35	3.75	30.69	40.91
HDL	9	29.19	1.40	26.51	31.11
PDL	9	67.23	2.23	64.77	72.48
DFPV	10	29.56	2.56	24.44	34.41
DFAN	10	24.85	1.00	22.77	26.26
DFCD	10	37.53	2.00	34.65	40.00
AFCD	10	28.35	1.93	25.56	31.33
HDD	9	22.76	1.65	20.00	25.56
DFCD	10	37.53	2.00	34.65	40.00
MAXCD	8	15.26	1.35	12.87	17.20
MINCD	10	12.75	0.90	10.89	13.76
PTAL	10	48.30	2.34	44.79	52.29
DFPT	10	46.69	2.47	42.22	49.54
MAXCD	7	53.10	6.34	39.02	64.29

Paratypes. YPM specimens 8710, 8735, 8736, 8737, 8738, 8739, 8741, 8742, 8744, 8757, 8759, 8760, 8762, 8763, 8854, 8864, 8869, 8871, 8872, 8880, 8881, 8980

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. For Virginia Reed Engbers McCune, in recognition of her contributions to the field work for this study

Description. Dorsal ridge scales are convex and almost triangular in dorsal view. The spines of these scales taper smoothly from their base to tip and increase in length posteriorly along the series. The last scale in the series is a large oval plate that abuts the first (unpaired) fulcrum on the leading edge of the dorsal fin. The total number of scales in the dorsal series, including the predorsal scale, is 18–19.

The moderately fusiform body and slender caudal peduncle of this species are most clearly seen by inspection of the outline drawings (Figs. 5, 13A). The slope of the forehead with respect to horizontal is about 35–40°.

There are 33–40 (mean = 35) lateral line scales. Fin positions relative to scales are as follows: The pelvic fins originate between the 7th and 10th vertical scale rows; the anal fin between rows 17–21; and the dorsal fin between rows 18–26, but always one or more scale rows behind the anal fin. Rarely (YPM 8854, 8871), there are intercalated scale rows dorsal to the lateral line and anterior to the dorsal fin. Scales are largest in the anterior flank region near the lateral line, decreasing in size both caudally and anterodorsally. Along the dorsal and ventral midline of the caudal peduncle the scales are enlarged. From the lateral line, there are 7–10 horizontal scale rows to the dorsal fin and 7–11 rows to the origin of the anal fin.

Both dorsal and anal fins are fringed with 6–8 fulcra; the first three are basal fulcra, and the bases of the next two lie against the unsegmented portion of the first lepidotrichium. Dorsal and anal lepidotrichia number 9–12 and 8–11, respectively. The pectoral and pelvic fins are fringed by at least 5–7 fulcra. Pelvic lepidotrichia number 3–6, and pectoral lepidotrichia number from 15–17.

Table 11. Parameter values of the regressions and correlation coefficients for *Semionotus virginiae*. For MAXCD, the independent variable is AFCD; for all other dependent variables, the independent variable is SL.

Variable	N	Y intercept	Slope	Correlation coefficient
DPTH	9	1.43	0.20	0.31
HDL	9	-0.32	0.33	0.91
PDL	9	-0.92	0.76	0.94
PAL	9	-0.15	0.75	0.93
DFPV	10	-0.54	0.35	0.73
DFAN	10	0.25	0.24	0.86
DFCD	10	0.25	0.35	0.79
AFCD	10	0.41	0.24	0.68
HDD	9	1.06	0.12	0.57
MAXCD	8	-0.03	0.15	0.49
MINCD	10	-0.16	0.14	0.76
PTAL	10	-1.12	0.60	0.91
DFPT	10	-0.93	0.56	0.89
MAXCD	17	0.31	0.42	0.55

Although the posterior margins of fins are often difficult to see, the tips of lepidotrichia extend at least beyond the tip of the last fin fulcrum. When appressed to the body, the posterior margin of the dorsal fin reaches to or beyond the region of the caudal peduncle where the median scales begin to enlarge, about halfway between the dorsal and caudal fins (YPM 8738, 8864). The caudal fin is more deeply forked than in other species of this group (Fig. 5A, YPM 8741, 8736) except *S. thomsoni*. The pectoral fins are not sufficiently well preserved to assess their length, but in YPM 8738 the pelvic fins reach just to the origin of the anal fin when appressed to the body. Similarly, the tip of the anal fin just reaches the origin of the caudal fin.

Table 12. Summary of meristic data for *Semionotus virginiae*

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
VDSC	13	8.4	0.8	7.0	10.0
VVSC	13	8.8	1.3	7.0	11.0
PLVSC	18	8.7	0.7	7.0	10.0
ANFSC	18	18.9	0.9	17.0	21.0
DFSC	18	21.3	1.6	18.0	26.0
CDSC	15	34.7	1.7	33.0	40.0
AXSC	11	8.9	1.1	7.0	10.0
PCTR	4	16.0	0.8	15.0	17.0
PLVR	6	4.5	1.2	3.0	6.0
ANFR	8	9.0	1.2	8.0	11.0
DFR	7	10.9	1.1	9.0	12.0
CDDR	7	8.9	0.4	8.0	9.0
CDVR	10	8.1	0.6	7.0	9.0
DFF1	8	3.5	0.5	3.0	4.0
DFF2	6	5.0	0.9	4.0	6.0
DFF3	6	7.3	0.8	6.0	8.0
AFF1	6	2.8	0.4	2.0	3.0
AFF2	6	4.3	0.5	4.0	5.0
AFF3	7	7.1	0.9	6.0	8.0
PCTF	2	6.0	1.4	5.0	7.0
PLVF	6	4.8	0.8	4.0	6.0
CDF	3	8.7	2.3	6.0	10.0
CVF	7	8.3	1.0	7.0	10.0

Semionotus thomsoni, new species

Figs. 5, 6, 7, 14A, 14B, 40; Tables 1, 2, 3, 13, 14, 15, 32

Diagnosis. *S. thomsoni* is a slender-bodied species, though deeper bodied than *S. kirschi* (Figs. 6, 7). It differs from both *S. kirschi* and *S. virginiae* by its more forwardly placed dorsal fin and long, slender tail; the body narrows more rapidly posterior to the dorsal fin than in either of the two other slender species in the *S. bergeri* group. *S. thomsoni* may be distinguished from *S. kirschi* by greater values for HDD, DFCD, MINCD, DFAN, MAXCD, and DPTH, all relative to standard length. In *S. thomsoni*, both the distance between the dorsal fin and the base of the axial lobe of the tail and that between the dorsal fin and the pectoral fin are greater than in *S. virginiae*. The caudal fin of *S. thomsoni* is forked, distinguishing it from all other members of the *S. bergeri* group except *S. virginiae*. The predorsal length in the former is shorter than the latter. A classification function is given in Table 1. For identification, the outline drawings (Figs. 5, 7, 14A) and regression equations for individual measurements against standard length (Table 14) are provided.

Holotype. YPM 8746 (P4-2668) complete fish, part and counterpart, negatively prepared (Fig. 40)

Paratypes. YPM specimens 6522, 8680, 8745, 8747, 8748, 8750, 8751, 8752, 8753, 8754, 8755, 8764, 8765, 8767, 8768, 8769, 8865, 8878, 8883, 8898

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. For K. S. Thomson, in gratitude for his advice and support throughout this study

Description. The dorsal ridge scales of *S. thomsoni* are simple and, in dorsal view, convex. The anterior scales may be almost triangular in shape, the bases of the spine tapering smoothly to the tips. Posteriorly, the spines elongate and there is a constriction between the scale base and the spine. The last scale in the series is a large oval plate that abuts the first fulcrum on the leading edge of the dorsal fin. The total number of scales in the dorsal series, including the predorsal scale, is about 20.

This species is among the more slender species of *Semionotus* with simple dorsal ridge scales (Fig. 14A); its shape is described quantitatively relative to the shapes of other species by a classification function given in Table 1. Summary statistics and the regression equations for individual measurements versus standard length are summarized in Tables 13 and 14. The fins, except the slightly anteriorly placed dorsal fin, are positioned as in other semionotids. The slope of the forehead with respect to horizontal is about 30–40°.

There are 31–36 (mean = 34) lateral line scales. The pelvic fin originates between the 7th and 10th vertical scale row, the anal fin between rows 16–20, and the dorsal fin between rows 19–22 but always one or more scale rows behind the anal fin. Consistent with the anteriorly placed dorsal fin is the fact that the upper end of the range of vertical scale rows anterior to the dorsal fin is truncated in *S. thomsoni* relative to the species most similar in shape (19–22, mean = 20.5, in *S. thomsoni* versus 18–26, mean = 21.3, in other *Semionotus*). About half of the specimens examined had intercalated scale rows dorsal to the lateral line and anterior to the dorsal fin. As in other *Semionotus*, the scales are largest in the

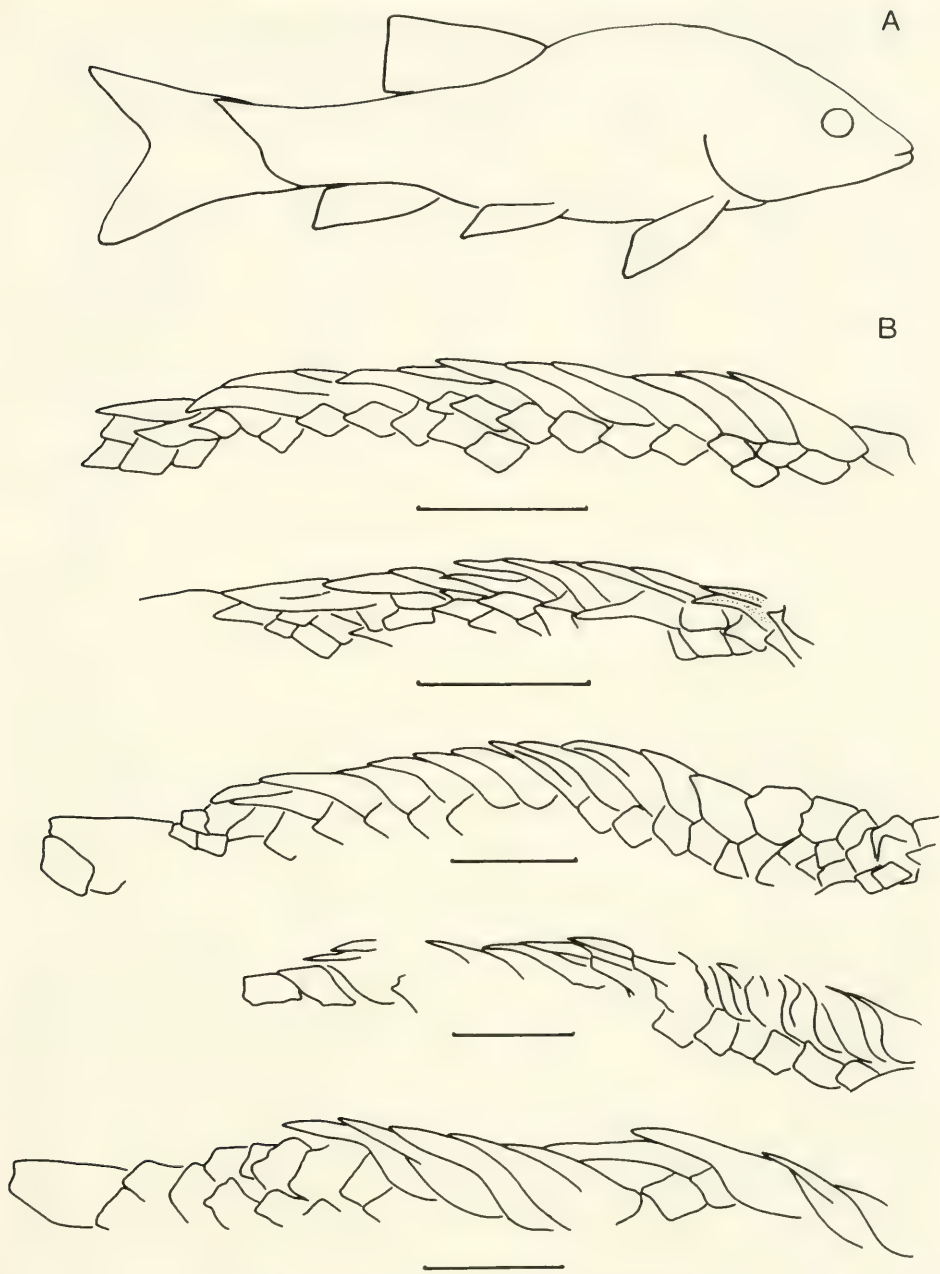


FIG. 14. *S. thomsoni*. A, outline of body form traced from YPM 8753, fins based on YPM 8752 and 8754; B, dorsal ridge scales of YPM 8746, 8750, 8680, 8767, 8752. Scale = 5 mm.

anterior flank region and around the lateral line. They decrease in size both caudally and anterodorsally. The scales along the dorsal and ventral midline of the caudal peduncle are enlarged. From the lateral line, there are 8–10 scales to the dorsal fin and 7–10 to the origin of the anal fin.

The dorsal and anal fins are fringed, with 5–8 and 6–9 fulcra respectively; usually the first three are basal fulcra and the bases of the next two lie against the unsegmented portion of the first lepidotrichium. There are 10–13 dorsal and 8–10 anal lepidotrichia. The pectoral and pelvic fins are fringed by up to 7 fulcra.

Table 13. Summary of morphometric data of *Semionotus thomsoni*. MAXCD expressed as % AFCD. All other variables but SL expressed as % SL.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
SL	11	9.74	1.42	7.20	11.50
DPTH	10	32.48	2.04	28.92	35.29
HDL	11	30.07	2.02	25.88	33.71
PDL	11	61.05	2.03	58.41	64.13
DFPV	10	25.98	1.84	23.53	28.57
DFAN	11	28.96	2.13	25.84	31.78
DFCD	11	43.89	2.30	39.13	46.73
AFCD	11	27.78	1.09	25.51	29.41
HDD	10	24.53	2.03	21.24	27.06
DFCD	11	43.89	2.30	39.13	46.73
MAXCD	11	14.59	0.79	13.04	15.29
MINCD	11	13.24	1.20	10.84	15.22
PTAL	11	45.86	2.04	43.82	50.00
DFPT	11	37.70	2.36	34.51	40.96
MAXCD	15	52.52	2.85	45.45	56.00

Pelvic lepidotrichia number 3–6 and pectoral lepidotrichia number 13–16. Meristic data are summarized in Table 15.

It is unclear how far the lepidotrichia extend beyond the last fin fulcrum, because distally the lepidotrichia become very delicate. The anal fin reaches the beginning of the ventral caudal fulcrum (YPM 8754). The posterior margin of the dorsal fin extends about halfway between the origins of the dorsal and caudal fins (YPM 8745), and the tip of the caudal fin appears to be forked (YPM 8752). The pectorals and pelvic fins, when appressed to the body, reach back as far as the pelvis and the anal fin, respectively (YPM 8752, 8754).

Semionotus euthenius, new species

Figs. 5, 6, 7, 15A, 15B, 41; Tables 1, 2, 3, 16, 17, 18, 32

Diagnosis. *S. euthenius* (Fig. 15A) is neither as slender as *S. kirschi*, *S. virginiae*, or *S. thomsoni* nor as deep bodied as *S. olseni*, *S. schaefferi*, or *S. redfieldii* (the last two are described below). The most similarly shaped species of the *S. bergeri* group as seen by visual inspection are also the species that occupy neighboring

Table 14. Parameter values of the regressions and correlation coefficients for *Semionotus thomsoni*. For MAXCD, the independent variable is AFCD; for all other dependent variables, the independent variable is SL.

Variable	N	Y intercept	Slope	Correlation coefficient
DPTH	10	-0.01	0.33	0.87
HDL	11	0.06	0.29	0.85
PDL	11	0.87	0.51	0.96
PAL	11	0.05	0.74	0.98
DFPV	10	0.17	0.24	0.80
DFAN	11	-0.37	0.33	0.85
DFCD	11	-0.47	0.48	0.91
AFCD	11	-0.47	0.26	0.93
HDD	10	0.70	0.17	0.68
MAXCD	11	0.12	0.13	0.86
MINCD	11	-0.02	0.13	0.75
PTAL	11	0.13	0.44	0.91
DFPT	11	0.79	0.29	0.81
MAXCD	15	0.13	0.48	0.79

Table 15. Summary of meristic data for *Semionotus thomsoni*

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
VDSC	10	9.2	0.8	8.0	10.0
VVSC	9	9.2	0.8	8.0	10.0
PLVSC	15	8.8	0.9	7.0	10.0
ANFSC	16	18.8	1.1	16.0	20.0
DFSC	16	20.5	1.2	19.0	22.0
CDSC	15	34.5	1.4	31.0	36.0
AXSC	9	9.3	1.0	8.0	10.0
PCTR	3	14.7	1.5	13.0	16.0
PLVR	9	4.7	1.3	3.0	6.0
ANFR	9	9.0	0.9	8.0	10.0
DFR	10	11.8	0.9	10.0	13.0
CDDR	3	9.0	0.0	9.0	9.0
CDVR	6	8.0	0.0	8.0	8.0
DFF1	15	3.4	0.5	3.0	4.0
DFF2	13	5.0	0.6	4.0	6.0
DFF3	10	7.2	1.0	5.0	8.0
AFF1	7	2.9	0.4	2.0	3.0
AFF2	6	4.8	0.4	4.0	5.0
AFF3	10	6.9	1.1	6.0	9.0
PCTF	6	6.0	0.6	5.0	7.0
PLVF	8	5.3	0.7	4.0	6.0
CDF	1	8.0	—	8.0	8.0
CVF	2	8.5	0.7	8.0	9.0

regions of multivariate space (Fig. 6). These species are *S. virginiae*, *S. thomsoni*, *S. olseni*, and *S. redfieldii*. Differences among them are characterized in the classification functions (Table 1) and illustrated by outline drawings of this species (Fig. 7) and others. The differences can also be identified by a series of regression equations (Table 17) compared with analogous equations with each other species. *S. euthenius* is deeper bodied than *S. virginiae*. However, the difference in maximum body depth is only slight; the distinction is more evident in the depth of the head, the distance between the dorsal and anal fins (essentially a depth measurement), and the maximum depth of the caudal peduncle. The principal distinction between *S. euthenius* and *S. thomsoni* is the difference in position of the dorsal fin as evidenced by the greater length of DFCD and the shorter length of PDL in *S. thomsoni*. In addition, the maximum depth of the caudal peduncle and maximum body depth of *S. euthenius* are greater than in *S. thomsoni*. Both *S. olseni* and *S. redfieldii* are deeper-bodied species than *S. euthenius*. The first has greater values for the measurements DPTH, DFAN, MINCD, DFCD, and HDD, all relative to standard length. *S. redfieldii* shows greater values for the measurements HDD, DFPV, MINCD, DFPT, MAXCD, and DPTH, all relative to standard length. Perhaps the species most similar in shape to *S. euthenius* is *S. kapffi*, from the Middle Keuper near Stuttgart, West Germany. The shapes of these two are almost identical, although the latter has a narrower caudal peduncle, a slightly deeper body, and a different distribution of the number of lateral line scales. In a sample of 25 individuals of *S. euthenius*, the mean number of lateral line scales was 34.6 (range = 32–38) whereas the mean number of lateral line scales in *S. kapffi* is 32.3 (range = 32–33 in a sample of 6). Furthermore, only one individual of *S. euthenius* had 32 lateral line scales and only four had 33 lateral line scales.

Holotype. YPM 8804 (P4-2644) complete fish, negatively prepared (Fig. 41)

Paratypes. YPM specimens 8756, 8801, 8802, 8803, 8806, 8808, 8809, 8812,

8813, 8814, 8815, 8816, 8817, 8819, 8820, 8822, 8823, 8824, 8825, 8826, 8827, 8828, 8829, 8830, 8831, 8832, 8839, 8867, 8868, 8870, 8873, 8896, 8900, 8910

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. From *euthenia*, which means abundance

Description. The dorsal ridge scales of *S. euthenius* are convex in dorsal view. The scale base may be slightly undercut lateral to the spine, and the spines increase in length posteriorly. The last scale in the series is a large oval plate that abuts the first fulcrum on the leading edge of the dorsal fin. The total number of scales in the dorsal series, including the predorsal scale, is about 20.

The classification function (Table 1) describes the shape of this species relative to the shapes of other closely related species. However, using the classification function for identification can be unwieldy, so individual measurements (Table 16) and regression equations are summarized. The overall shape is most clearly seen by inspection of the outline drawings (Figs. 5, 15A) and comparison of this shape with others (Fig. 7). The fins are placed as in other semionotids. The forehead slopes at about 40–50° relative to horizontal.

There are 32–38 (mean = 35) lateral line scales. The pelvic fin originates between the 7th and 10th vertical scale row, the anal fin between rows 16–21, and the dorsal fin between rows 19–24 but always one or more scale rows behind the anal fin. Meristic data are summarized in Table 18. About half the individuals examined had intercalated scale rows in the epaxial region anterior to the dorsal fin. Flank scales are largest anteriorly and near the lateral line; they decrease in size both caudally and anterodorsally. Posteriorly, on the caudal peduncle, the median dorsal and ventral scales are enlarged. From the lateral line, there are 8–12 scales to the dorsal fin and 7–11 to the origin of the anal fin.

The dorsal and anal fins are fringed with up to 9 fulcra; usually the first three are basal fulcra and the bases of the next two lie against the unsegmented portion of the first lepidotrichium. There are 10–13 dorsal and 8–12 anal lepidotrichia. The pectoral and pelvic fins are fringed by at least 5–8 fulcra. Pelvic lepidotrichia number 3–8 and pectoral lepidotrichia number from 14–17. In all fins, the tips of the lepidotrichia are difficult to see but extend at least beyond the tip of the last fin fulcrum. The posterior margin of the dorsal fin extends posteriorly to about the middle of the caudal peduncle, where the median scales begin to enlarge (YPM 8824, 8816). The caudal fin is weakly emarginate (YPM 8816). When appressed to the body, the pectoral fins extend almost to the pelvic fins (YPM 8824), and the tips of the pelvics just reach the origin of the anal fin (YPM 8817). The anal extends almost to the beginning of the caudal fin (YPM 8824).

Semionotus convalis, new species

Figs. 5, 6, 7, 16A, 16B, 41; Tables 1, 2, 3, 32

Diagnosis. The body form of this species is very distinct (Figs. 5, 16A). Not only is it rather deep bodied through the trunk region for its size, but both the head and tail are almost as deep as the body itself. On the basis only of maximum body depth relative to standard length, there could be no confusion of this species with any other species of the *S. bergeri* group, with the exception of *S. schaefferi*. However, the maximum depth of the caudal peduncle (MAXCD) in *S. convalis* is greater than that of any other species including *S. schaefferi*. There are no

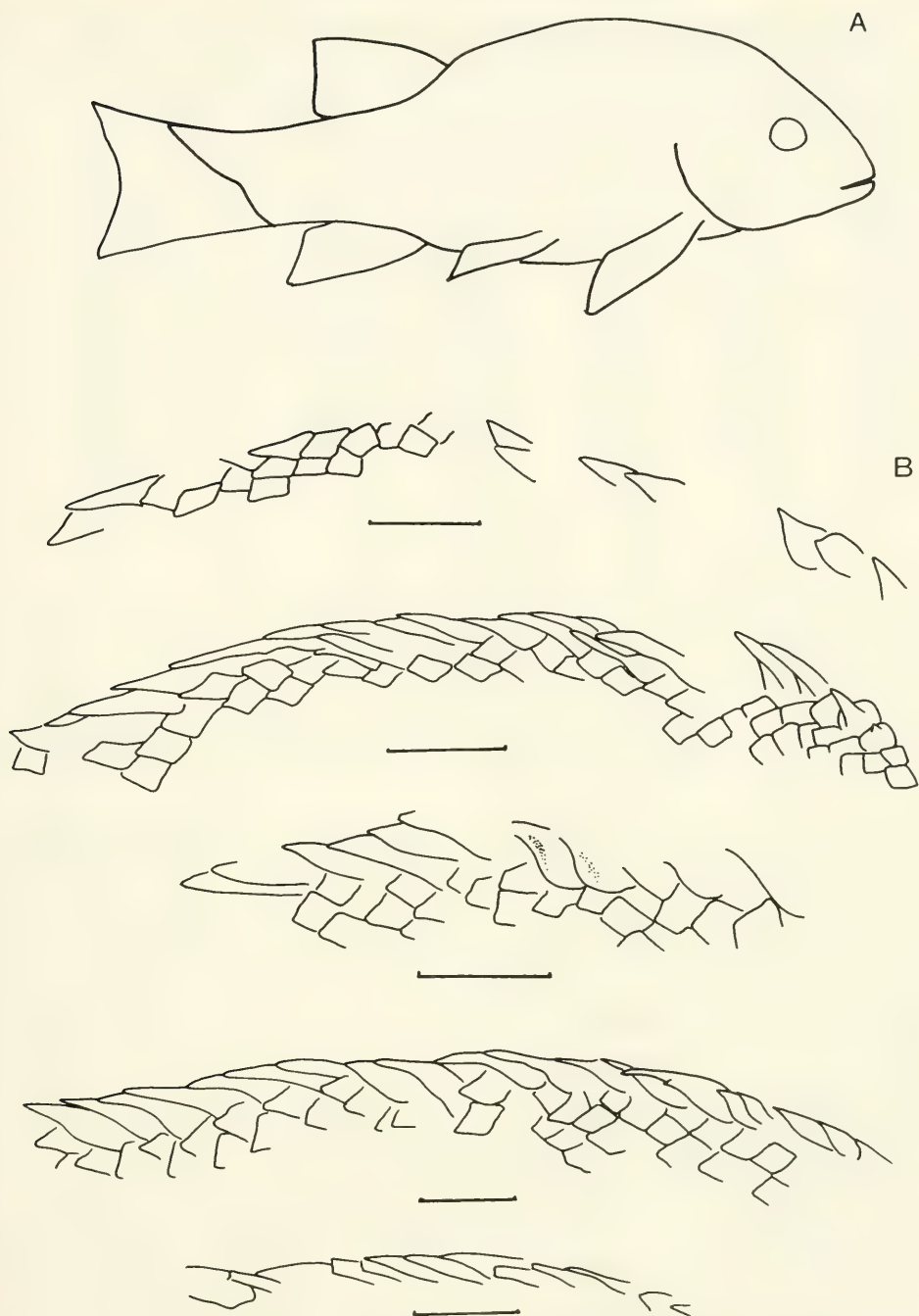


FIG. 15. *S. euthenius*. A, outline of body form traced from YPM 8804, fins based on YPM 8816, 8824, and 8817; B, dorsal ridge scales of YPM 8804, 8815, 8814, 8854, 8827. Scale = 5 mm.

regression lines for comparison between the single specimen of *S. convalis* and other species. However, a series of bivariate plots for each variable against standard length for all species of the *S. bergeri* group described here show that the distance from the dorsal fin to the base of the epaxial lobe of the tail (DFCD) and the distance from the tip of the snout to the origin of the anal fin (PAL) in this individual is outside the range for all other species. Relative to the deep-bodied

Table 16. Summary of morphometric data of *Semionotus euthenius*. MAXCD expressed as % AFCD. All other variables but SL expressed as % SL.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
SL	22	9.36	1.05	7.30	11.90
DPTH	20	36.91	1.85	32.69	41.10
HDL	21	30.19	1.17	28.05	33.00
PDL	21	66.28	2.21	61.54	70.79
DFPV	18	31.06	2.28	28.57	36.99
DFAN	21	28.55	1.49	25.93	31.58
DFCD	21	39.81	2.28	34.69	44.21
AFCD	22	28.30	2.24	25.00	33.33
HDD	20	26.93	2.21	23.23	32.88
DFCD	21	39.81	2.28	34.69	44.21
MAXCD	20	17.25	1.63	14.74	20.55
MINCD	21	13.91	1.33	11.58	17.81
PTAL	19	46.47	2.63	42.22	50.56
DFPT	18	44.64	2.46	40.38	48.78
MAXCD	22	61.42	6.26	46.67	74.07

forms, *S. schaefferi* and *S. redfieldii*, the distance between the snout and the origin of the dorsal fin is shorter in *S. convalis* (see Fig. 7).

The extraordinary depth of the head in this species is not reflected in the measurements taken, because the unusual aspect of form is how far anteriorly the head remains deep and head depth is measured posteriorly. For identification, an outline drawing (Fig. 16A) and the classification function (Table 1) are provided.

Holotype. YPM 8770 (P4-1955) complete fish, part and counterpart, negatively prepared (Fig. 41)

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Table 17. Parameter values of the regressions and correlation coefficients for *Semionotus euthenius*. For MAXCD, the independent variable is AFCD; for all other dependent variables, the independent variable is SL.

Variable	N	Y intercept	Slope	Correlation coefficient
DPTH	20	0.27	0.34	0.83
HDL	21	0.03	0.30	0.87
PDL	21	0.72	0.59	0.88
PAL	22	-0.49	0.79	0.94
DFPV	18	0.60	0.25	0.59
DFAN	21	0.05	0.28	0.79
DFCD	21	-0.11	0.41	0.75
AFCD	22	0.45	0.23	0.60
HDD	20	0.82	0.18	0.55
MAXCD	20	0.57	0.11	0.36
MINCD	21	0.31	0.10	0.51
PTAL	19	-0.66	0.39	0.74
DFPT	18	0.55	0.39	0.74
MAXCD	22	-0.04	0.62	0.92

Table 18. Summary of meristic data for *Semionotus euthenius*

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
VDSC	18	9.6	1.2	8.0	12.0
VVSC	19	8.8	0.9	7.0	10.0
PLVSC	26	8.6	0.8	7.0	10.0
ANFSC	31	19.1	1.2	16.0	21.0
DFSC	27	21.2	1.3	19.0	24.0
CDSC	25	34.6	1.4	32.0	38.0
AXSC	11	9.1	0.9	8.0	10.0
PCTR	8	16.1	1.1	14.0	17.0
PLVR	12	4.9	1.4	3.0	8.0
ANFR	17	9.7	0.9	8.0	12.0
DFR	18	11.4	0.9	10.0	13.0
CDDR	10	8.9	0.3	8.0	9.0
CDVR	12	8.0	0.0	8.0	8.0
DFF1	17	3.1	0.3	3.0	4.0
DFF2	15	4.9	0.5	4.0	6.0
DFF3	15	6.8	0.9	5.0	8.0
AFF1	9	2.8	0.4	2.0	3.0
AFF2	9	4.8	0.4	4.0	5.0
AFF3	18	6.9	0.9	5.0	9.0
PCTF	9	5.7	0.7	5.0	7.0
PLVF	9	5.8	1.1	5.0	8.0
CDF	6	8.8	1.3	8.0	11.0
CVF	12	8.9	1.2	8.0	12.0

Etymology. From *convallis*, meaning glen, for the valley in which the P4 excavation site is located

Description. The dorsal ridge scales of *S. convallis* are simple, dorsally convex, and almost triangular in shape (Fig. 16B). The scale spines increase in length posteriorly, but all scales taper smoothly from the base to the spine tip. The last scale in the series is a large oval plate that abuts the first (unpaired) fulcrum on the leading edge of the dorsal fin. There are 18 scales in the dorsal series, including the predorsal scale.

The body form of this species is very distinctive. Not only is it rather deep bodied through the trunk region for its size, but both the head and tail are almost as deep as the body itself. The head does not really begin to taper anteriorly until almost the orbit, whereas in other semionotids, the body begins to taper well before the nape and continues down onto the forehead. The slope of the forehead with respect to horizontal is about 50°. The caudal peduncle, though very long (as shown by DFC/D relative to standard length), is so deep that it gives the fish an appearance of having a very short tail. The classification function (Table 1) describes shape relative to all others quantitatively. In the plot of the first two canonical variables (Fig. 6), this individual lies well outside all other groups. The form of this species is so unusual that it can be readily identified from an outline drawing (Fig. 16A).

In the only known individual of this species, there are 36 lateral line scales. The pelvic fin originates at the 9th vertical scale row, the anal fin at row 17, and the dorsal fin at row 20. There are no intercalated scale rows dorsal to the lateral line and anterior to the dorsal fin in the single specimen of this species. Flank scales are largest in the anterior flank region and around the lateral line. They decrease in size both caudally and anterodorsally. The dorsal and ventral median scales on the caudal peduncle are enlarged. From the lateral line, there are 10 scales to the dorsal fin and 10 to the origin of the anal fin.

The dorsal fin is fringed with 6 fulcra, the anal fin with 8; in both cases, the

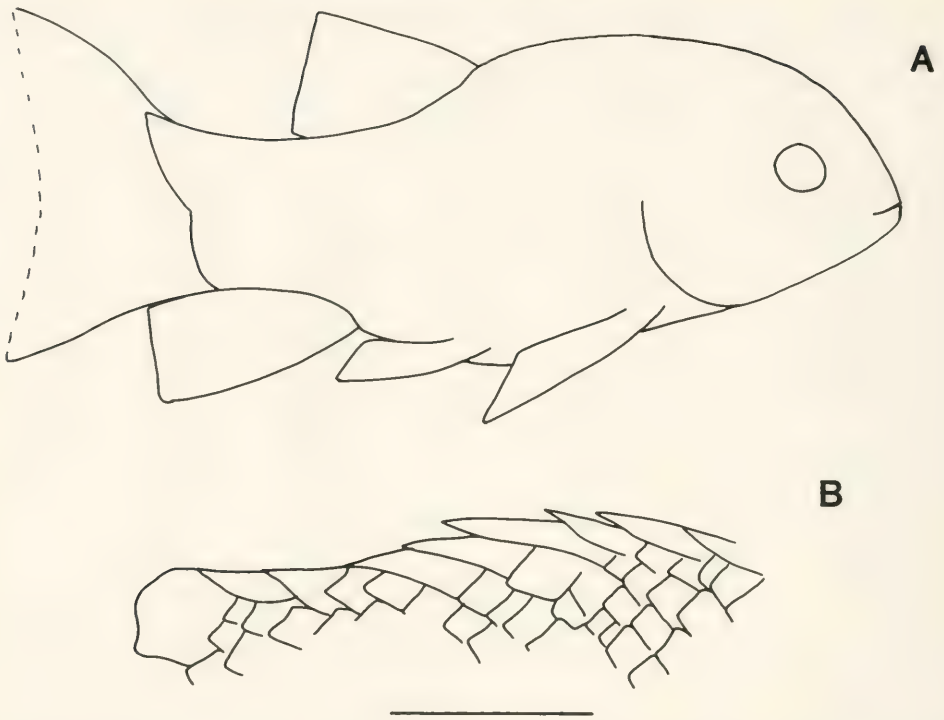


FIG. 16. *S. convalis*. A, outline of body form traced from YPM 8770; B, dorsal ridge series of YPM 8770. Scale = 5 mm.

first three are basal fulcra and, at least in the anal fin, the bases of the next two lie against the unsegmented portion of the first lepidotrichium. There are 13 dorsal and 9 anal lepidotrichia. Each of the pectoral fins has at least 13 lepidotrichia, fringed by at least 6 fulcra. Pelvic lepidotrichia number 5, and the fin is fringed by at least 4 fulcra. In all fins, the lepidotrichia extend beyond the tip of the last fulcrum. The fins are well enough preserved in the holotype to see that the rays of the pectoral fins extend back as far as the origin of the pelvic fins. The pelvics reach to the origin of the anal fin, and the anal extends as far as the caudal fin. The tip of the dorsal fin reaches about half the length of the caudal peduncle.

Semionotus redfieldii, new species

Figs. 5, 6, 7, 17A, 17B, 41; Tables 1, 2, 3, 19, 20, 21, 32

Diagnosis. *S. redfieldii* is a fairly deep-bodied species, more so than all other species of *Semionotus* in the *S. bergeri* group except *S. schaefferi* and *S. convalis*. The closest species in shape are *S. schaefferi*, *S. euthenius*, and *S. olseni*. It differs from *S. euthenius* by being slightly deeper in DPTH, HDD, MAXCD and MINCD, DFPV, and DFPT. *S. redfieldii* is also slightly deeper bodied than *S. olseni*. In addition to depth variables, other measurements that differentiate *S. redfieldii* from *S. olseni* are the greater DFPV, greater MAXCD, and the shorter DFCD. The shape of *S. redfieldii* differs from that of *S. schaefferi* most significantly in body depth, but there are also slight differences in the DFCD, the MAXCD, MINCD, and the DFAN. In addition, the dorsal ridge scales of *S. schaefferi* are more elaborate than those of *S. redfieldii* (see description of *S. schaefferi* below).

Holotype. YPM 8772 (P4-1910) complete fish, mechanically prepared (Fig. 41)

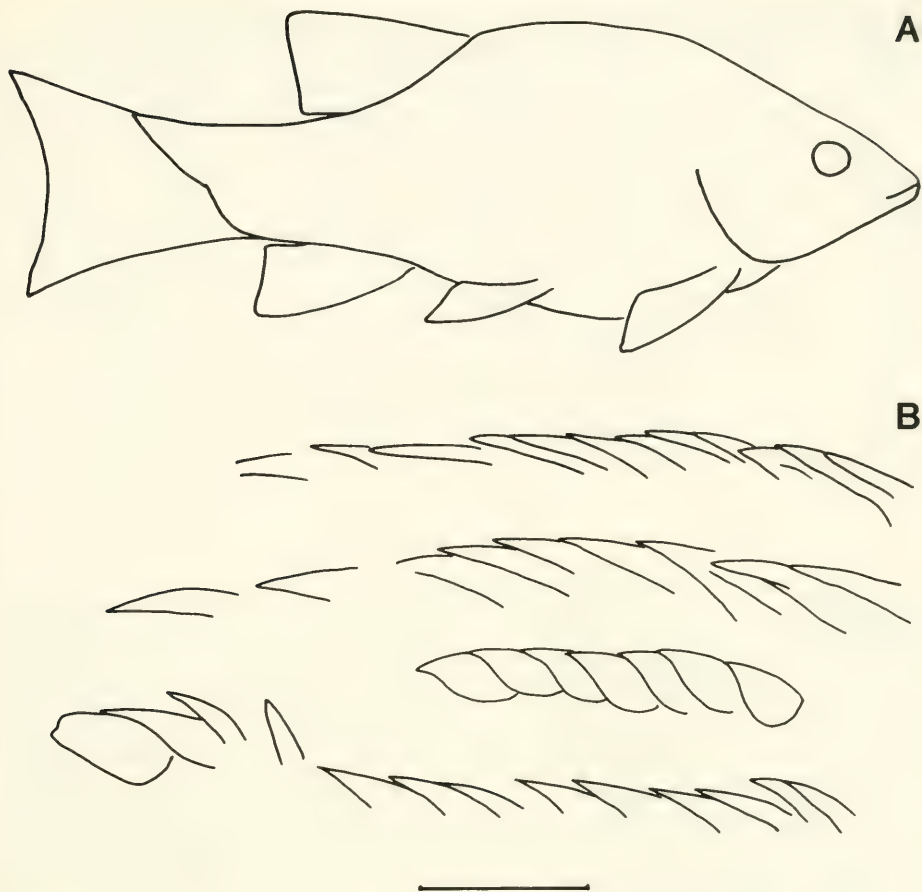


FIG. 17. *S. redfieldii*. A, outline of body form traced from YPM 8778, fins based on YPM 8791; B, dorsal ridge scales of YPM 8772, 8784, 8785, 8786. Scale = 5 mm.

Paratypes. YPM specimens 8771, 8773, 8774, 8775, 8776, 8777, 8778, 8779, 8780, 8781, 8782, 8783, 8784, 8785, 8786, 8787, 8788, 8790, 8791, 8793, 8794, 8795, 8911

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. For W. C. and J. H. Redfield, pioneers of Newark paleoichthyology

Description. The dorsal ridge scales of *S. redfieldii* are convex and almost triangular in dorsal view (Fig. 17B). Along the entire series, the scales taper smoothly from the scale base to the tip of the spines, the spines increasing in length posteriorly. The last scale in the series is a large oval plate that abuts the first (unpaired) fulcrum on the leading edge of the dorsal fin. The total number of scales in the dorsal series, including the predorsal scale, is about 19.

This species is among the more deep bodied of *Semionotus* with simple dorsal ridge scales (Figs. 6, 7). The classification function (Table 1) describes the shape of this species relative to others included in the analysis. For identification, outline drawings of this species (Figs. 5, 17A), summary statistics (Table 19) and regression equations (Table 20) are provided. The fins are placed approximately

Table 19. Summary of morphometric data of *Semionotus redfieldii*. MAXCD expressed as % AFCD. All other variables but SL expressed as % SL.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
SL	10	8.61	1.23	7.10	11.10
DPTH	10	45.46	2.91	42.25	50.45
HDL	10	31.87	2.26	28.17	34.48
PDL	9	69.82	2.71	66.67	74.32
DFPV	6	38.99	2.72	35.44	43.66
DFAN	9	32.28	2.96	29.11	36.94
DFCD	9	39.76	1.95	36.62	43.24
AFCD	10	32.07	2.82	27.59	36.94
HDD	9	29.69	1.45	27.27	31.96
DFCD	9	39.76	1.95	36.62	43.24
MAXCD	8	21.18	1.39	18.75	22.78
MINCD	9	17.65	2.04	14.94	21.62
PTAL	10	46.85	3.30	42.05	52.25
DFPT	9	51.54	3.00	46.39	55.86
MAXCD	10	63.54	6.83	53.57	78.26

as in all other semionotids, and the caudal peduncle is rather slender. The slope of the forehead with respect to horizontal is about 35–45°.

Lateral line scales number 33–37 (mean = 35). The pelvic fin originates between the 7th and 10th vertical scale row, the anal fin between rows 17–20, and the dorsal fin between rows 19–24 but always one or more scale rows behind the anal fin. Meristic data are summarized in Table 21. No known specimens of this species have intercalated scale rows. The largest flank scales are those in the anterior region near the lateral line. They decrease in size both caudally and anterodorsally. Both dorsal and ventral median scales on the caudal peduncle are large relative to lateral caudal scales. From the lateral line, there are 9–11 scales to the dorsal fin and 8–10 to the origin of the anal fin.

The dorsal and anal fins are fringed with 6–8 fulcra; usually the first two or three are basal fulcra, and the bases of the next two lie against the unsegmented portion of the first lepidotrichium. There are 10–12 dorsal and 9–10 anal lepidotrichia. No specimens give a reliable count for pectoral fulcra or lepidotrichia, but the pelvic fins are composed of 3–8 lepidotrichia and fringed by at least 5 fulcra. In all fins, the tips of the lepidotrichia extend beyond the tip of the last fin fulcrum. The posterior margin of the dorsal fin reaches at least to the region where the scales along the dorsal midline of the caudal peduncle begin to enlarge, or about halfway between the dorsal and caudal fins (YPM 8791). In this same specimen, the tips of the pectorals are not well preserved, but the pelvics extend back almost to the anal fin, and the anal to the caudal fin. The caudal fin is weakly emarginate (YPM 8791).

SPECIES WITH MODIFIED SIMPLE SCALES

Semionotus schaefferi, new species

Figs. 5, 6, 7, 18A, 18B, 41; Tables 1, 2, 3, 22, 23, 24, 32

Diagnosis. This species is more deep bodied than all species of *Semionotus* with simple dorsal ridge scales (Figs. 5, 6, 18A). *S. schaefferi* differs from *S. redfieldii*, the species most similar in shape, by having a deeper body (DPTH) and caudal peduncle (MAXCD) relative to standard length (Fig. 7). In addition, *S. schaefferi*

Table 20. Parameter values of the regressions and correlation coefficients for *Semionotus redfieldii*. For MAXCD, the independent variable is AFCD; for all other dependent variables, the independent variable is SL.

Variable	N	Y intercept	Slope	Correlation coefficient
DPTH	10	-1.00	0.57	0.91
HDL	10	-0.87	0.42	0.94
PDL	9	0.15	0.68	0.94
PAL	10	-0.91	0.84	0.97
DFPV	6	0.63	0.31	0.71
DFAN	9	-1.19	0.46	0.90
DFCD	9	-0.89	0.50	0.97
AFCD	10	-0.63	0.40	0.79
HDD	9	-0.13	0.31	0.91
MAXCD	8	-0.05	0.22	0.85
MINCD	9	-0.79	0.27	0.81
PTAL	10	-1.09	0.60	0.89
DFPT	9	-0.40	0.56	0.87
MAXCD	10	0.35	0.50	0.74

has a pronounced dorsal hump, whereas the back of *S. redfieldii* is almost flat between the dorsal fin and the nape. Consistent with its great body depth, the number of horizontal scale rows from the lateral line to the dorsal fin and from the lateral line ventral to the anal fin is greater in *S. schaefferi* than in any other species. There are also slight differences in the DFAN, the DFCD, and the MAXCD, MINCD. Perhaps the greatest distinguishing feature of this species, however, is the form of the dorsal ridge series (Fig. 18B). All the scales in the series have spines, though they are short anteriorly and elongate posteriorly. Like simple dorsal ridge scales, the scales of *S. schaefferi* are dorsally convex but the dorsal surface is not entirely covered by ganoine. The area covered by ganoine is the same shape as the scale itself but smaller, so that there is a rim of "naked" bone around the perimeter of the scale (Fig. 18B).

Table 21. Summary of meristic data for *Semionotus redfieldii*

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
VDSC	4	10.3	1.0	9.0	11.0
VVSC	4	9.5	1.0	8.0	10.0
PLVSC	14	8.3	0.8	7.0	10.0
ANFSC	13	18.6	1.1	17.0	20.0
DFSC	15	21.4	1.5	19.0	24.0
CDSC	12	35.0	1.5	33.0	37.0
AXSC	5	9.6	1.5	7.0	11.0
PCTR	0	-	-	-	-
PLVR	3	4.7	2.1	3.0	7.0
ANFR	3	9.3	0.6	9.0	10.0
DFR	5	11.0	0.7	10.0	12.0
CDDR	2	9.0	0.0	9.0	9.0
CDVR	5	8.2	0.4	8.0	9.0
DFF1	7	3.1	0.4	3.0	4.0
DFF2	7	5.1	0.4	5.0	6.0
DFF3	5	7.8	0.4	7.0	8.0
AFF1	3	3.0	1.0	2.0	4.0
AFF2	3	5.7	0.6	5.0	6.0
AFF3	3	7.3	1.2	6.0	8.0
PCTF	0	-	-	-	-
PLVF	3	5.0	0.0	5.0	5.0
CDF	1	10.0	-	10.0	10.0
CVF	1	12.0	-	12.0	12.0

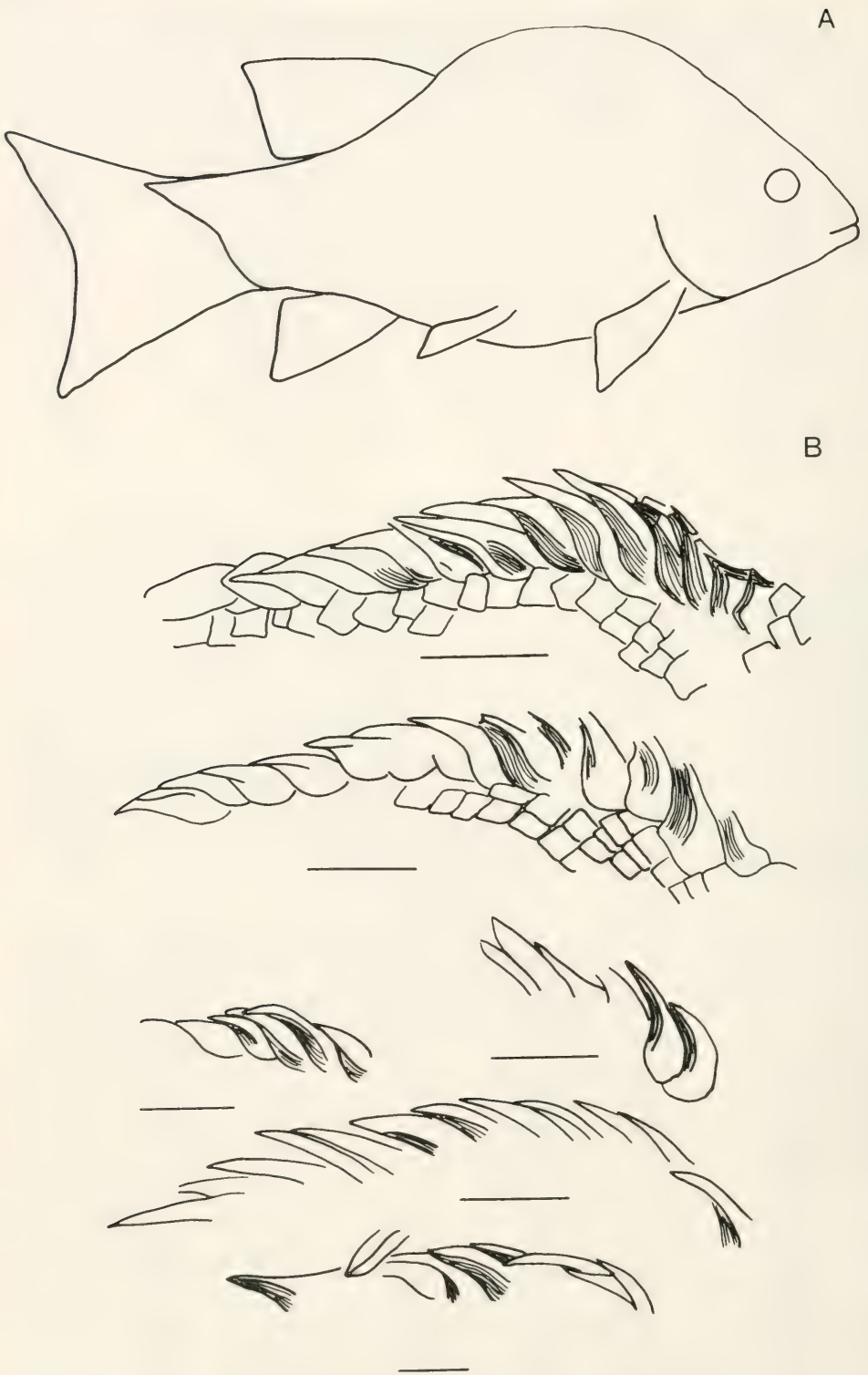


FIG. 18. *S. schaefferi*. A, outline of body form traced from YPM 6587, fins based on YPM 8893 and 8796; B, dorsal ridge scales of YPM 8856, 8912, 8918, 8915, 8918, 8903, 8914. Scale = 5 mm.

Table 22. Summary of morphometric data of *Semionotus schaefferi*. MAXCD expressed as % AFCD. All other variables but SL expressed as % SL.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
SL	11	8.01	1.12	5.90	9.40
DPTH	10	53.40	6.17	46.74	66.10
HDL	9	31.19	2.70	26.60	35.62
PDL	10	70.14	3.52	66.28	76.27
DFPV	8	40.91	3.62	35.87	46.97
DFAN	7	38.49	4.42	33.70	46.97
DFCD	10	44.66	3.47	40.96	51.52
AFCD	8	30.34	1.85	28.26	32.93
HDD	10	31.98	3.96	27.17	40.91
DFCD	10	44.66	3.47	40.96	51.52
MAXCD	8	22.08	1.70	19.57	24.24
MINCD	11	19.66	2.86	15.28	25.42
PTAL	8	45.84	1.98	42.47	48.94
DFPT	10	51.80	3.74	45.83	59.32
MAXCD	11	72.28	8.07	57.14	84.21

Holotype. YPM 8856 (P4-1878) complete fish, part and counterpart, negatively prepared (Fig. 41)

Paratypes. YPM specimens 6534, 6580, 6587, 8796, 8798, 8799, 8857, 8858, 8859, 8862, 8893, 8903, 8912, 8914, 8915, 8916, 8917, 8918

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. For Bobb Schaeffer, in recognition of his outstanding and numerous contributions to ichthyology, especially his studies on fossil fishes from the Newark Supergroup

Description. The dorsal ridge scales of *S. schaefferi* are convex in dorsal view, but only the centers of the scales are covered in ganoine (Fig. 18B). The spines on the dorsal ridge scales are short anteriorly and longer posteriorly. The last scale in the series is a large oval plate that abuts the first fulcrum on the leading edge of the dorsal fin. The total number of scales in the dorsal series, including the predorsal scale, is 18.

As this species is the most deep-bodied *Semionotus* species having simple scales, it is easy to recognize. For identification, an outline drawing of this species (Fig. 18A), summary statistics (Table 22), regression equations (Table 23), and a classification function (Table 1) are provided. The fins are placed approximately as in all other semionotids, and the caudal peduncle, like the trunk, is rather deep. The forehead slopes at an angle of about 50–65° relative to horizontal.

There are 33–37 (mean = 35) lateral line scales. The pelvic fin originates between the 7th and 9th vertical scale row, the anal fin between rows 16–20, and the dorsal fin between rows 18–23 but always one or more scale rows behind the anal fin. Meristic data are summarized in Table 24. Occasionally, there are intercalated scale rows dorsal to the lateral line and anterior to the dorsal fin (YPM 8862, 8799, 8856, 8915). The scales are largest in the anterior flank region and near the lateral line. They decrease in size both caudally and anterodorsally. Both dorsal and ventral median scales on the caudal peduncle are large relative

Table 23. Parameter values of the regressions and correlation coefficients for *Semionotus schaefferi*. For MAXCD, the independent variable is AFCD; for all other dependent variables, the independent variable is SL.

Variable	N	Y intercept	Slope	Correlation coefficient
DPTH	10	2.03	0.27	0.55
HDL	9	0.54	0.24	0.67
PDL	10	0.62	0.62	0.90
PAL	7	0.68	0.65	0.91
DFPV	8	0.38	0.36	0.64
DFAN	7	0.90	0.27	0.47
DFCD	10	0.39	0.40	0.78
AFCD	8	0.06	0.30	0.79
HDD	10	1.50	0.13	0.20
MAXCD	8	0.61	0.14	0.60
MINCD	11	0.44	0.14	0.39
PTAL	8	0.86	0.57	0.95
DFPT	10	0.75	0.42	0.82
MAXCD	11	0.75	0.42	0.83

to the lateral caudal scales. From the lateral line, there are 10–13 scales to the dorsal fin and 10–12 to the origin of the anal fin.

The dorsal and anal fins are fringed with 6–8 and 6–9 fulcra, respectively; the first three are basal fulcra, and the bases of the next two lie against the unsegmented portion of the first lepidotrichium. There are 10–12 dorsal and 8–11 anal lepidotrichia. The pectoral and pelvic fins are fringed by at least 6–7 fulcra. There are 4 pelvic lepidotrichia and 17 pectoral lepidotrichia. In all fins, the tips of the lepidotrichia extend beyond the last fin fulcra. The posterior margin of the dorsal fin extends about halfway between the dorsal and caudal fins (YPM 8893). The tips of the pectoral fins are not clear in any specimens, but the tips of the pelvic fins extend as far back as the anal fin, and the anal fin in turn extends as far back as the beginning of the caudal fin (YPM 8796). The shape of the caudal fin is ambiguous, but it appears to be weakly emarginate, as in most other species in the genus.

Semionotus anosteus, new species

Figs. 19A, 19B, 42; Table 32

Diagnosis. *S. anosteus* is distinguished from all other species of *Semionotus* by the greater length of its head relative to standard length, its forwardly placed dorsal fin (Fig. 19A), and the morphology of its dorsal ridge scales (Fig. 19B).

Holotype. YPM 8844 (P4-2611) complete fish, counterpart lacks tail (Fig. 42); both part and counterpart negatively prepared

Paratypes. YPM 8851, 8866

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. From *osteon* (= bone), meaning without bone; named for the holotype specimen, negatively prepared in acid

Description. The dorsal ridge scales of *S. anosteus* are dorsally convex, but they are not as simple as those of the *S. bergeri* group (Fig. 20B). Anteriorly, the well-

Table 24. Summary of meristic data for *Semionotus schaefferi*

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
VDSC	3	11.7	1.5	10.0	13.0
VVSC	3	10.7	1.2	10.0	12.0
PLVSC	10	8.2	0.8	7.0	9.0
ANFSC	10	17.7	1.5	16.0	20.0
DFSC	10	20.3	1.3	18.0	23.0
CDSC	11	34.5	1.3	33.0	37.0
AXSC	5	10.6	1.7	8.0	12.0
PCTR	3	17.0	0.0	17.0	17.0
PLVR	4	4.0	0.0	4.0	4.0
ANFR	5	9.4	1.3	8.0	11.0
DFR	7	11.3	1.0	10.0	12.0
CDDR	5	8.6	0.5	8.0	9.0
CDVR	9	8.1	0.3	8.0	9.0
DFF1	9	3.1	0.3	3.0	4.0
DFF2	7	5.0	0.6	4.0	6.0
DFF3	10	7.2	0.6	6.0	8.0
AFF1	4	3.0	0.0	3.0	3.0
AFF2	4	5.0	0.0	5.0	5.0
AFF3	7	7.9	0.9	7.0	9.0
PCTF	4	6.5	0.6	6.0	7.0
PLVF	2	6.0	0.0	6.0	6.0
CDF	1	9.0	—	9.0	9.0
CVF	2	11.5	0.7	11.0	12.0

developed spines are fully supported by a bony base. Only the spine and the center of the scale are covered by ganoine; the lateral aspect of the bony base of the scale is not covered by ganoine. Posteriorly, the spines become longer and narrower, but they are still more robust than in *Semionotus melanimus* or *Semionotus latheticus*. The last scale in the series is a large oval plate that abuts the first (unpaired) fulcrum on the leading edge of the dorsal fin. The total number of scales in the dorsal series, including the predorsal scale, is about 19.

The overall shape of this species is fusiform (Fig. 19A), but relative to other species in the *S. bergeri* group, it has an unusually large head. It is most similar in shape to *Semionotus johberryi*, but in addition to a longer head, its dorsal fin is positioned more anteriorly. The forehead slopes at an angle of about 30° relative to horizontal.

In the holotype, there are 33 lateral line scales. The pelvic fin originates at the 7th scale row, the anal fin at row 19, and the dorsal fin at row 21. In the holotype, there are no intercalated scale rows dorsal to the lateral line and anterior to the dorsal fin. The largest flank scales are in the anterior region near the lateral line. They decrease in size both caudally and anterodorsally. On the caudal peduncle, both the dorsal and ventral median scales are larger than lateral scales. From the lateral line, there are 9 scales to the origin of the anal fin.

The dorsal and anal fins are fringed with 8–10 fulcra; the first three of these are basal fulcra, and the bases of the next two lie against the unsegmented portion of the first lepidotrichium. The number of dorsal lepidotrichia is unclear, but there are 9 anal lepidotrichia. The pelvic fins consist of 4 lepidotrichia fringed by 9 fulcra. The pectoral fins are not well preserved in the holotype. In all fins, the tips of the lepidotrichia extend beyond the tip of the last fin fulcrum. The posterior margin of the dorsal fin extends about halfway between the dorsal and caudal fins (YPM 8866). The anal fin and the pelvic fins almost reach the origin of the caudal fin and anal fin, respectively (YPM 8844, 8866). The tips of the pectoral fins are not visible in any specimen.

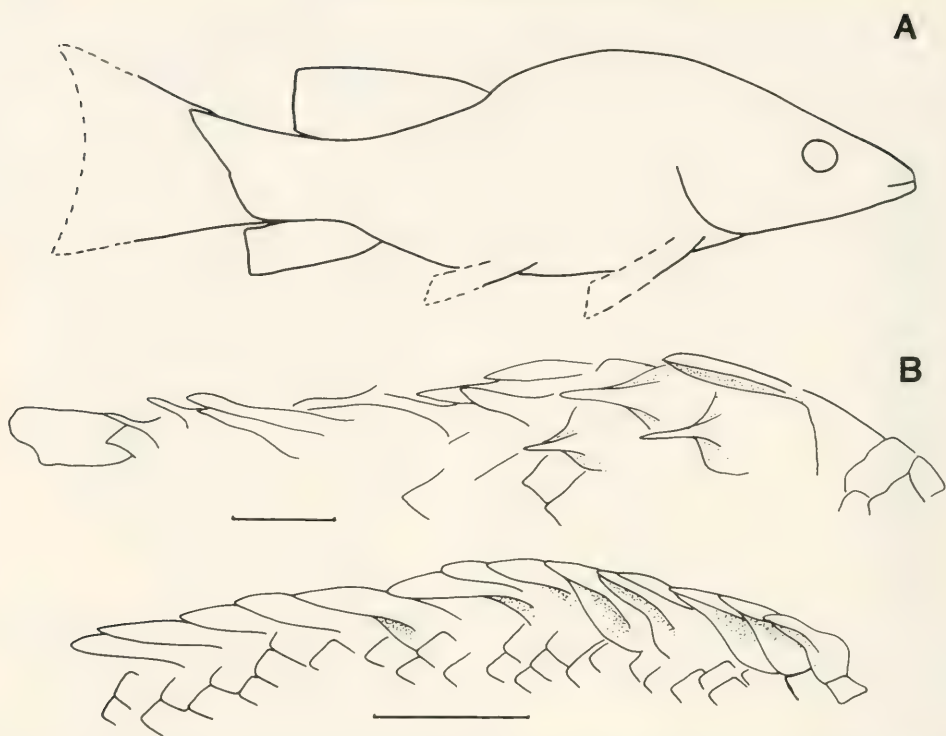


FIG. 19. *S. anosteus*. A, outline of body form traced from YPM 8844; B, camera lucida drawing of the dorsal ridge scales of YPM 8851 (top) and YPM 8844 (bottom). Scale = 5 mm.

SPECIES WITH SMALL SCALES

Semionotus amplicephalus

Figs. 20A, 20B, 42; Table 32

Diagnosis. The body form of this species differs from all species of the *S. bergeri* group in that the length of the head is much larger relative to standard length, about 33% (Fig. 20A). In addition, this species is distinguished from the *S. bergeri* group by the morphology of its dorsal ridge scales (Fig. 20B). As in many other species of *Semionotus*, the scales of *S. amplicephalus* are dorsally convex and have posteriorly directed spines. However, the spines of the first eleven scales are very short relative to the size of the scale base, and the dorsal ridge scales are no larger than the flank scales. This distinctive dorsal ridge scale morphology has been termed the "small scale" type (Olsen and others 1982).

Holotype. YPM 8849 (P4-2442) almost complete fish; partial counterpart; both negatively prepared (Fig. 42)

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. From *amplus*, meaning large, and *cephal*, meaning head

Description. The dorsal ridge scales of this species are like those of the small-scale group (Olsen and others 1982). These scales have short, thin spines (Fig.

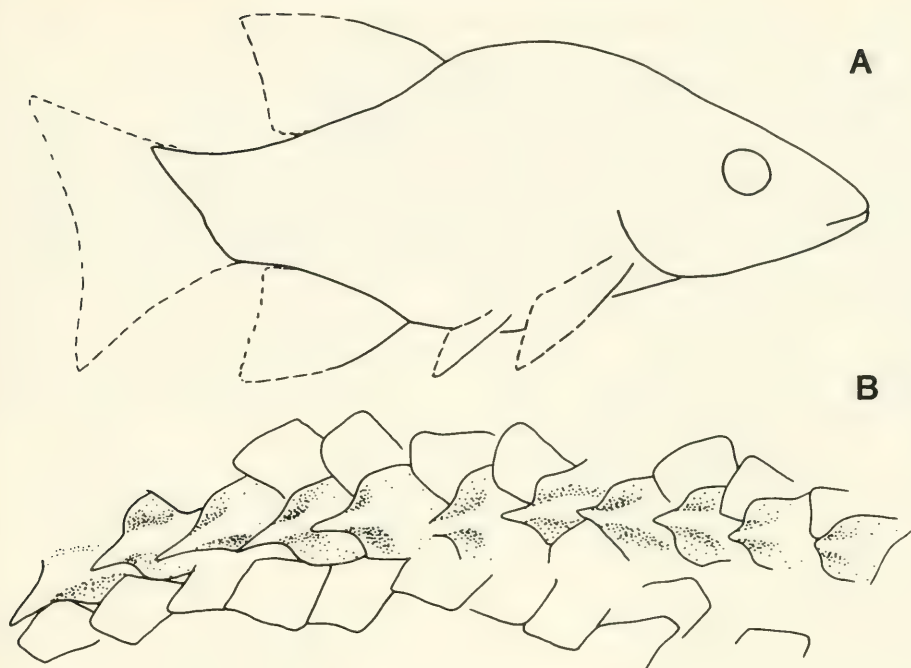


FIG. 20. *S. amplicephalus*. A, outline of body form; B, camera lucida drawing of dorsal ridge scales. Scale = 5 mm. Both figures based on the holotype YPM 8849.

20B), and the scale bases are the same size or smaller than the flank scales. The holotype of this species is preserved in rock taken from the edge of a slump, and it may be somewhat distorted. However, what is unusual about its shape is that the head is very large in proportion to its body, and the probable direction of distortion would only make the fish appear more slender than it really is, not change the proportion of head to body length. The holotype is very large, about 29 cm standard length, and the head takes up an unusually large proportion of its length, about one-third. The body itself and the caudal peduncle are both stocky (Fig. 20A).

Neither the scales nor the fin rays are well enough preserved to count with confidence, but there appear to be about 13 vertical scale rows anterior to the pelvic fin and about 30 lateral line scales. These counts, though only from one individual, are out of the range of variation for most *Semionotus* and related genera. The fact that this individual is unusually proportioned, has low scale counts, and has unusual dorsal ridge scales justifies specific distinction even of this single individual.

The skull is quite well preserved, with a good view of the skull roof, a single suborbital, open cheek region, the circumorbital series, and the jaw joint, all as described for other Newark semionotids (Olsen and McCune ms).

Although I have designated no paratypes, I tentatively refer another specimen, collected by Redfield (YPM 6484), to this species. It is a large individual with a large head like the holotype, but its shape is too distorted for reliable measurement. I refer this specimen to *S. amplicephalus* on the basis of a single dorsal ridge scale, which is like that described above for *S. amplicephalus*, and the fact that the pelvic fins originate at about the 13th or 14th scale row.

SPECIES WITH THIN-SPINED SCALES

Semionotus latheticus, new species

Figs. 21A, 21B, 42; Table 32

Diagnosis. *S. latheticus* is a moderately deep-bodied species, very similar in shape to *S. olseni* (Fig. 21A). It is distinguished from the latter by the morphology of its dorsal ridge scale series (Fig. 21B), in which the spines are very long and slender relative to the scale base like those of the *Semionotus micropterus* group (Olsen and others 1982).

Holotype. YPM 8899 (P4-1994) complete fish, part and counterpart; one side negatively prepared; the other side, which shows the dorsal ridge scales in positive view, is not acid prepared (Fig. 42)

Paratype. YPM 8841

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. From *lathetic*, meaning likely to escape notice

Description. The dorsal ridge scale series of this species is very distinctive. Anteriorly, the bases of the scales are very round, and there is a long, very slender, posteriorly directed spine. Posteriorly, the spines are longer than they are on the anterior scales. The spine and only the central portion of the scale base are covered with ganoine (Fig. 21B). The last scale in the series, a large oval plate, abuts the first (unpaired) fulcrum on the leading edge of the dorsal fin. The total number of scales in the dorsal series, including the predorsal scale, is about 20.

The body form is similar to that of *S. olseni* (Fig. 21A). The body is somewhat deep, with a moderately thick caudal peduncle. The slope of the forehead with respect to horizontal is about 45°. The only paratype, YPM 8841, is not complete, so although the existing portion is consistent with the holotype, it is not definitively the same shape. However, this individual differs in shape from the other two known species having the same type of dorsal ridge scale series.

In the holotype, there are 34 lateral line scales. The pelvic, anal, and dorsal fins originate at the 8th, 17th, and 19th scale rows, respectively. The scales in the anterodorsal flank region are not clear enough to determine whether there are intercalated scale rows. The scales are largest in the anterior flank region and around the lateral line. They decrease in size both caudally and anterodorsally. The scales along the dorsal and ventral midline of the caudal peduncle are larger than the lateral caudal scales. In the holotype, there are 13 scales between the lateral line and the dorsal fin, and 10 from the lateral line to the origin of the anal fin.

The total number of fulcra on the dorsal and anal fins is uncertain. The dorsal fin fulcra follow the usual Newark semionotid pattern in having three basal fulcra and two fringing fulcra lying against the unsegmented portion of the first lepidotrichium. Except in the pelvic fin, which has three lepidotrichia, the fins of the holotype are not well enough preserved to count fin rays.

In all fins, the tips of the lepidotrichia extend beyond the tip of the last fin fulcrum.

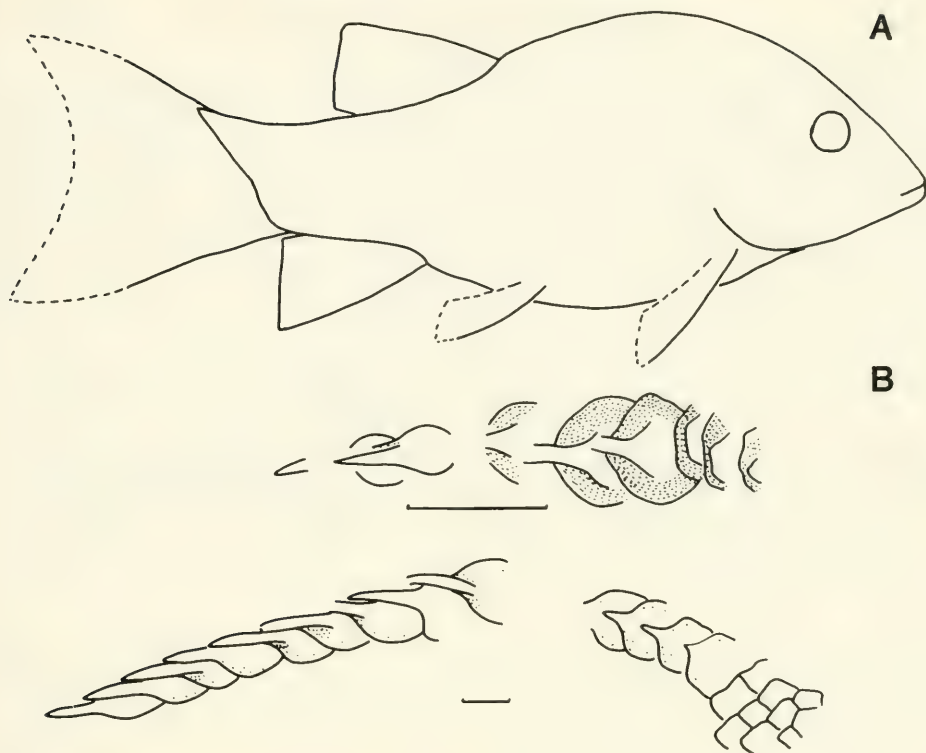


FIG. 21. *S. latheticus*. A, outline of body form traced from YPM 8899; B, camera lucida drawings of YPM 8899 (top) and YPM 8841 (bottom). Scale = 5 mm.

***Semionotus melanimus*, new species**

Figs. 22A, 22B, 42; Table 32

Diagnosis. *S. melanimus* has dorsal ridge scales similar to those of the *S. micropterus* group (Olsen and others 1982). The form of the caudal peduncle of this species is unusual among semionotids, as there is almost no constriction of the body posterior to the dorsal fin (Fig. 22A). Instead, the sides taper almost straight back to the minimum point at the posterior end of the caudal peduncle, the overall shape being more like a cone than an hourglass.

Holotype. YPM 8840 (P4-2368) complete fish, part and counterpart; one side negatively prepared (Fig. 42)

Paratypes. YPM specimens 8758, 8877, 8979

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. From *melanimum*, meaning black-clad, in reference to the black-colored bone characteristic of this and most fishes from the P4 excavation

Description. The dorsal ridge scales of this species are like those described for *S. latheticus*. Anteriorly, the bases of the scale are very round with long, very slender, posteriorly directed spines that are longer on posterior scales than on anterior

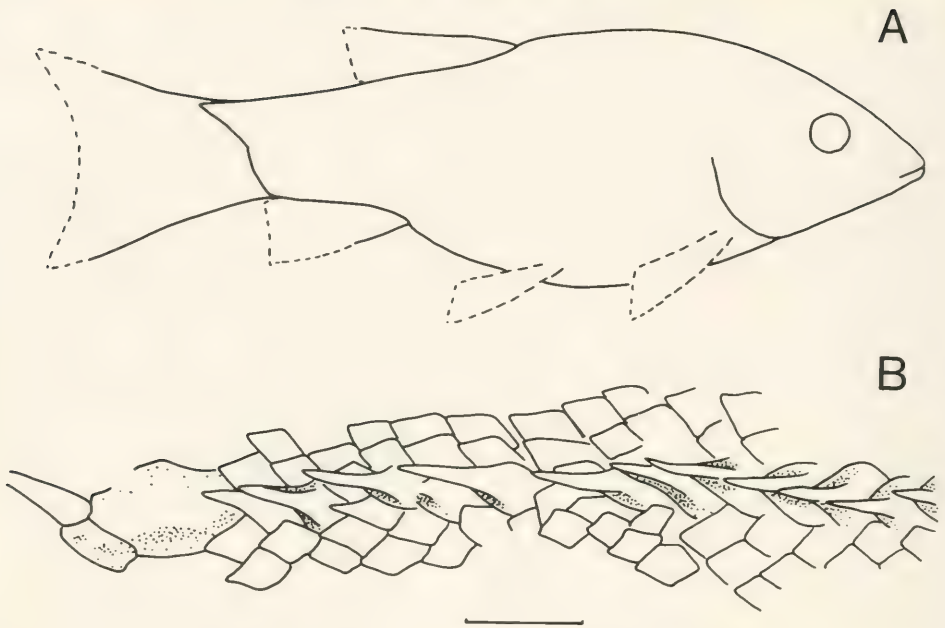


FIG. 22. *S. melaninus*. A, outline of body form traced from YPM 8840; B, camera lucida drawing of the dorsal ridge scales of YPM 8840. Scale = 5 mm.

scales. Only the spine and the central portion of the scale base are covered with ganoine (Fig. 22B). A large oval plate at the end of the series abuts the first (unpaired) fulcrum on the leading edge of the dorsal fin. The total number of scales in the dorsal series, including the predorsal scale, is about 19.

S. melaninus is a moderately deep-bodied species, with a large head and thick caudal peduncle tapering in an almost straight line from the dorsal and anal fins back to the minimum point of the caudal peduncle (Fig. 22A). The slope of the forehead with respect to horizontal is about 30–40°.

In the holotype, there are 38 lateral line scales. The origin of the pelvic fin is not visible in the holotype, but the anal fin originates at the 21st scale row, and the dorsal fin at row 24. At least in the holotype, there are intercalated scale rows dorsal to the lateral line and anterior to the dorsal fin. Near the lateral line, anterior flank scales are largest, decreasing in size both caudally and anterodorsally. In the caudal region, dorsal and ventral median scales are larger than lateral scales.

The dorsal fin is fringed with 8 fulcra; the first three are basal fulcra, and the bases of the next two lie against the unsegmented portion of the first lepidotrichium. There are 11 dorsal and 10 anal lepidotrichia in the holotype. The pelvic fins are not sufficiently well preserved to count fulcra or fin rays. The pectoral fin has 14 lepidotrichia, but the number of fulcra is uncertain. The caudal fin has 19 lepidotrichia, 10 of which insert dorsal to the lateral line. In all fins, the tips of the lepidotrichia extend beyond the tip of the last fin fulcrum. The caudal fin appears to be weakly emarginate (YPM 8979), as shown in Figure 22A. The tips of the dorsal and paired fins are not visible in any specimen, but as in other Newark semionotids, the anal fin reaches almost to the beginning of the caudal fin.

***Semionotus johberryi*, new species**

Figs. 23A, 23B, 42; Table 32

Diagnosis. This species is distinguished from most other species of *Semionotus* by the morphology of its dorsal ridge scales (Fig. 23B), which are similar to those of the *S. micropterus* group (Olsen and others 1982). The dorsal ridge scales of this species differ from other *S. micropterus* group scales in that the spines are wider and the supporting flange of bone not covered by ganoine is more robust. Compared with *S. melaninus* and *S. latheticus*, which also have *S. micropterus* group scales, *S. johberryi* is more slender in body form and its dorsal fin is more posterior. Compared with *S. anosteus*, which is most similar in body shape, the spines of *S. johberryi* are much broader and the flange of bone underneath the spine is much larger. In addition, the dorsal fin of *S. johberryi* is more posterior than that of *S. anosteus* and the caudal peduncle is thus shorter.

Holotype. YPM 8800 (P4-2612) complete fish, negatively prepared (Fig. 42); counterpart shows no detail

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. Named for John Strong Newberry, author of the classic monograph on semionotid fishes from Connecticut and New Jersey. Contraction of his first and last names was necessary because the name *Semionotus newberryi* has already been published (Loper 1893).

Description. The dorsal ridge scales are round at the base, with long, narrow spines on all but the first three or four scales (Fig. 23B). Certain features of the dorsal ridge scales, such as the roundness of the scale bases and the long, slender spines extending posteriorly well beyond the scale base resemble features of *S. micropterus* group scales (Olsen and others 1982). However, the spines on the dorsal ridge scales of YPM 8800 are supported by a bony extension of the scale base, whereas in fishes of the *S. micropterus* group the spines extend unsupported beyond the base. The spines on posterior scales are longer than they are on anterior scales. The last scale in the dorsal scale series is a large oval plate that abuts the first (unpaired) fulcrum on the leading edge of the dorsal fin. The total number of scales in the dorsal series, including the predorsal scale, is about 21.

The shape of this specimen is unique among the *Semionotus* complex (see Fig. 23A). It is probably most similar to that of *S. anosteus*, but in *S. johberryi* the body is deeper through the belly, the tail is shorter or the dorsal fin more posterior, and the head is shorter. The slope of the forehead relative to horizontal is about 30°.

In the holotype, there are 34 lateral line scales. The origin of the pelvic fin is not visible, but the anal fin originates at row 20 and the dorsal fin at row 21. In the holotype, a few intercalated scale rows are present dorsal to the lateral line and anterior to the dorsal fin. The scales are largest in the anterior flank region and near the lateral line. They decrease in size both caudally and anterodorsally. Dorsal and ventral median scales on the caudal peduncle are larger than lateral scales. From the lateral line, there are 8 scales to the dorsal fin and 7 to the origin of the anal fin.

The fin fulcra can be counted only on the anal fin, which has 7. Pelvic and

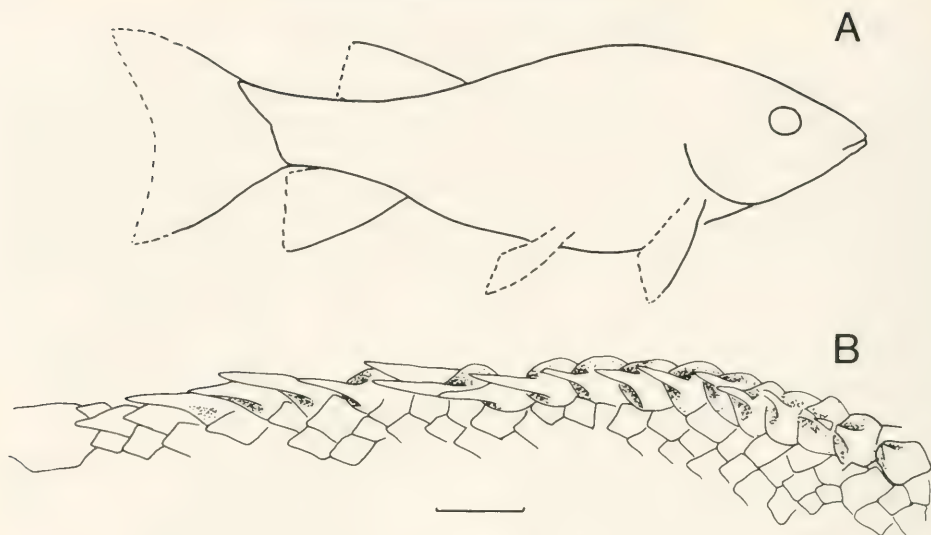


FIG. 23. *S. johberryi*. A, outline of body form traced from YPM 8800; B, camera lucida drawing of the dorsal ridge scales of YPM 8800. Scale = 5 mm.

pectoral lepidotrichia are not well preserved in the holotype, but in the dorsal and anal fins there are 15 and 10, respectively. The posterior portions of all fins are truncated well before their tips.

THE SEMIONOTUS TENUICEPS GROUP

One of the first semionotids from North America (Hitchcock 1819; Agassiz 1835), *S. tenuiceps* (Agassiz) is one of the most distinctive semionotids, distinguishable by its very elaborate dorsal ridge scales, previously termed robust or globular scales (Fig. 9E, F). Semionotids having such scales have been found in the Jurassic of both eastern North America and China (Olsen and others 1982). In North America, they have been found in the Turner's Falls Sandstone in the Deerfield Basin of Massachusetts; the Feltsville and Towaco Formations in the Newark Basin of New Jersey (Olsen and others 1982); and the Waterfall Formation in the Culpeper Basin of Virginia (Hentz 1981). From China, isolated robust dorsal ridge scales have been found in the lower Lufeng (Olsen and others 1982). The morphology of these elaborate dorsal ridge scales is sufficiently distinctive to suggest that semionotids having these scales form a monophyletic group. I refrain from giving this complex a formal subgeneric or generic designation, however, because to do so would result in *Semionotus* becoming paraphyletic. Instead, I refer informally to species in this group as the *S. tenuiceps* group.

The derived characters that unite members of this group are 1) anterior (beginning with 2nd to 6th), dorsal ridge scales greatly enlarged, 2) base of dorsal ridge scale accounting for bulk of scale, 3) spines on anterior dorsal ridge scales point dorsally before angling posteriorly, and 4) spines barely extending beyond the scale base.

Within the *S. tenuiceps* group there are three variants on the generally elaborate morphology of the dorsal ridge scale series.

The first pattern is best exemplified by *S. tenuiceps* (Fig. 24A). The first two scales are small and spineless, but beginning with about the third scale, there are

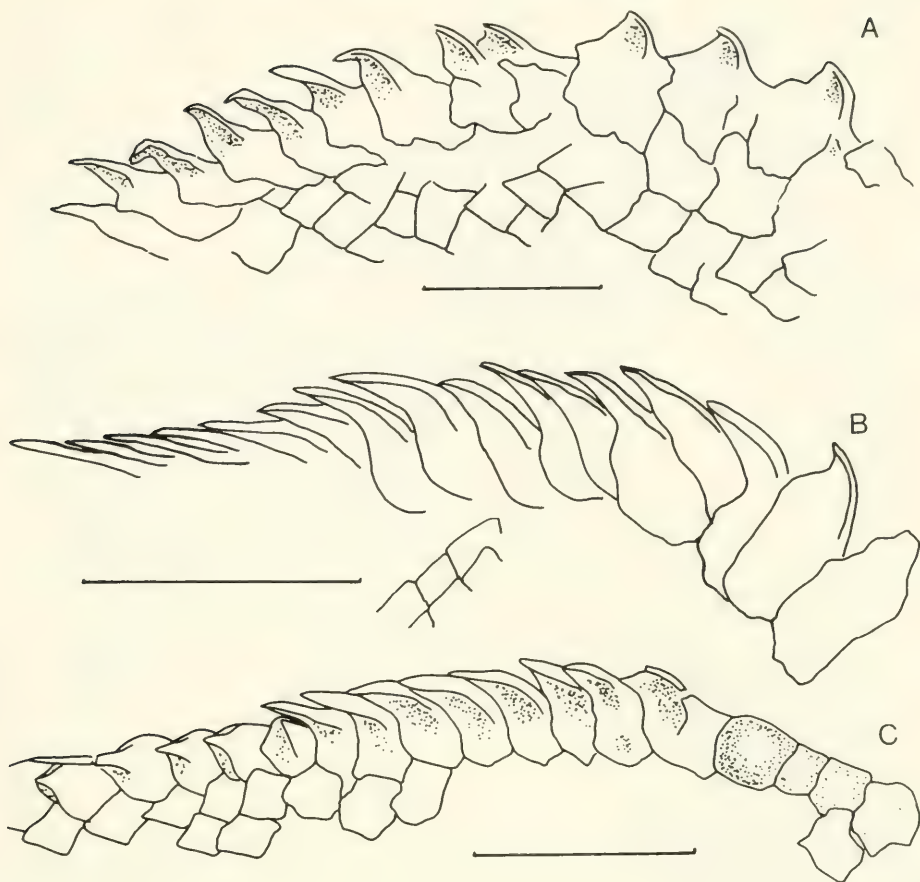


FIG. 24. Variation in dorsal ridge scales of the *S. tenuiceps* group. A, classic "*tenuiceps*" dorsal ridge scales; camera lucida drawing of the neotype, *S. tenuiceps*, YPM 8162; Sunderland, Massachusetts. B, hypermorphic "*tenuiceps*" dorsal ridge scales, YPM 6960; Turner's Falls, Massachusetts. C, moderate or globular "*tenuiceps*" dorsal ridge scales (YPM 8932); Yale excavation in Wayne, New Jersey. Note the size of the dorsal ridge scales relative to the flank scales in each type. Scale = 1 cm.

about 6 to 9 robust, angular scales. These scales are broad at the base in an anterior-posterior direction and 2 to 3 times the width of a normal flank scale. Dorsally and along an anterior-posterior axis, the spines are convex. In lateral view, they are undercut slightly beneath the spine and the bases of the scales expand ventrally. The posteriormost scales are simple and convex with well-developed spines, each one overlapping the scale behind it.

Very much like this robust series are hypermorphic scales, which differ from robust scales by their much larger size relative to flank scales and the fish itself (Fig. 24B). *Semionotus* with these exaggerated dorsal scales are known from the Feltville Formation in the Newark Basin (Olsen and others 1982) and the Turner's Falls Sandstone in the Deerfield Basin, but not from the Towaco Formation of the Newark Basin. Thus, no descriptions of species with hypermorphic scales are included here.

In a third version of the *S. tenuiceps*-type dorsal ridge scale series, the globular form, enlarged scales do not begin until about the 6th scale posterior to the extrascapulars (Fig. 24C). Fish with this moderate scale pattern seem to be missing the several most exaggerated scales (3rd to 6th) in the robust series. From about the 6th to 12th scales, the scale bases are large and bulbous and the spines point

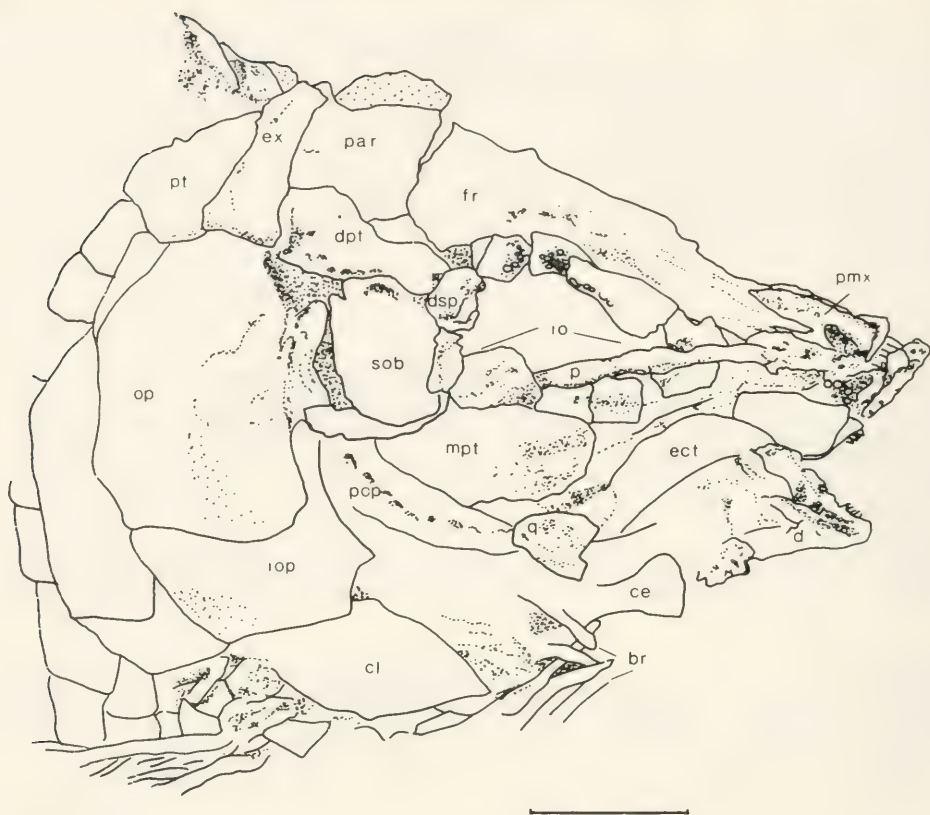


FIG. 25. Skull of *S. tenuiceps*. Camera lucida drawing of neotype, YPM 8162; Sunderland, Massachusetts. Scale = 1 cm. Abbreviations: br, branchiostegal rays; d, dentary; ce, ceratohyal; cl, cleithrum; dpt, dermopterotic; dsp, dermosphenotic; ect, ectopterygoid; ex, extrascapular; fr, frontal; io, infraorbital; iop, interopercular; mpt, metapterygoid; op, opercular; p, parasphenoid; par, parietal; pmx, premaxilla; pop, preopercular; pt, posttemporal; q, quadrate; sub, suborbital.

first dorsally, then posteriorly. Again, the posteriormost scales have flatter bases and longer spines, each one overlapping the scale behind.

Skull

The pattern of dermal bones in the skull of the *S. tenuiceps* group shows little deviation from the general pattern described for the *S. elegans* group (Olsen and McCune ms), and for *Semionotus* (Schaeffer and Dunkle 1950); it is described only briefly here. Skulls from individuals of two different species of the group, *S. tenuiceps* (Fig. 25), with robust dorsal ridge scales, and *Semionotus saginatus* (Fig. 26), with globular dorsal ridge scales, are figured here.

The skull roof shows the only deviation from the general Newark semionotid pattern. The parietals are rectangular, almost square, and join medially. The frontals are narrow anteriorly in the *S. tenuiceps* group (Olsen and McCune ms), and the *S. bergeri* group including *S. (Lepidotes) minor* (Woodward 1916-19; McCune 1986), and *Semionotus normanniae* (Larsonneur 1964). This contrasts to the broad frontals found in *Semionotus braunii* (Olsen and others 1982), *Lepidotes elvensis* (Deschaseaux 1943; Wenz 1967), *L. mantelli* (Woodward 1916-19) and *L. laevi* (MNHP 1917-05). In the *S. tenuiceps* group, the suture between the frontals is digitate as in the *S. elegans* group, but between the frontals and parietals the suture is almost straight rather than digitate as in the *S. elegans*

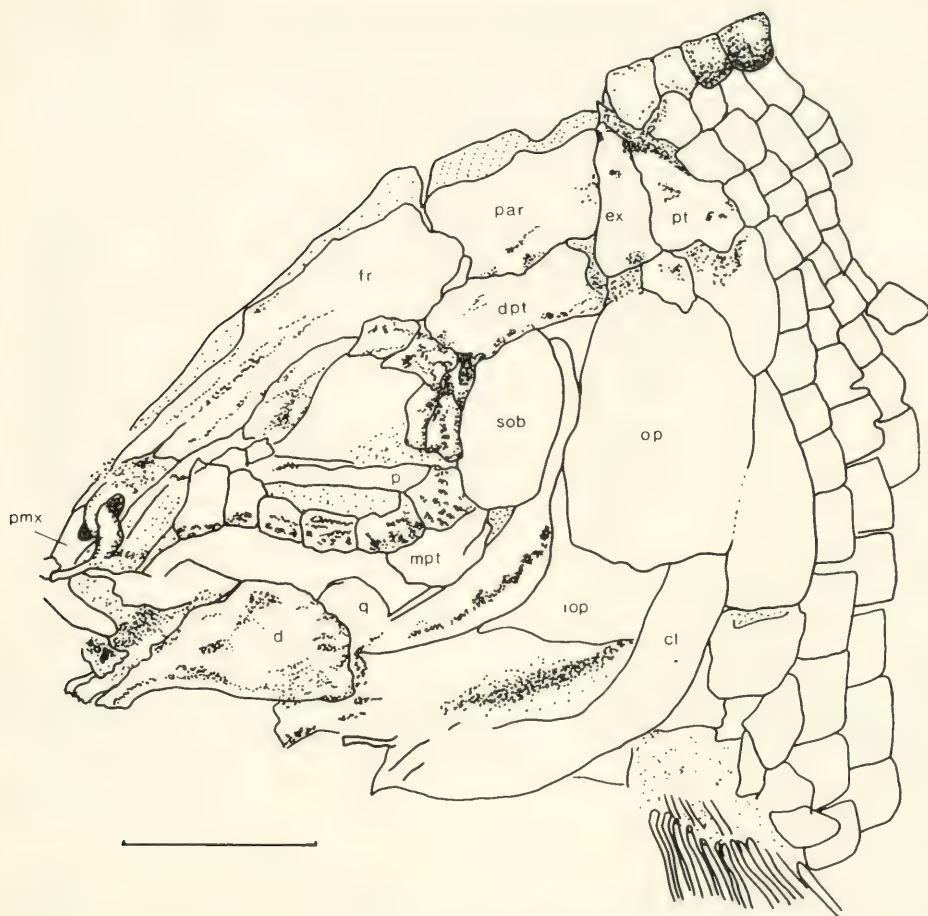


FIG. 26. Skull of *S. saginatus*. Camera lucida drawing of holotype, YPM 8932 from Yale P4 excavation in Wayne, New Jersey. Scale = 1 cm. For abbreviations, see legend for Fig. 25.

group (Olsen and McCune ms). The pattern of the snout is like that described for the *S. elegans* group (Olsen and McCune ms).

The circumorbital series is complete and composed of 2 or 3, usually 3, supraorbitals (which may or may not be tuberculated), the dermosphenotic, 5 or 6 infraorbitals, the lachrymal, and 2 infraorbitals between the lachrymal and the antorbital. The infraorbitals within the circumorbital ring seem to be slightly thinner than in the *S. elegans* group, but the lachrymal and anterior infraorbitals are similarly deep. The dermopterotic and the pattern of the lateral line canals are like those of the *S. elegans* group.

Like other non-*Lepidotes* semionotids, including the *S. elegans* group, *Semionotus capensis* (Olsen and McCune ms), *S. normanniae*, and *S. bergeri* (McCune 1982), the cheek region is completely open except for an oval suborbital positioned between the circumorbitals and preoperculum and below the dermopterotic. The jaw joint is like that described by Patterson (1973) for *L. toombsi*, and all other Newark semionotids (Olsen and McCune ms), *S. normanniae*, *S. bergeri* (McCune 1982). The palate, the hyoid arch, the opercular series, and the pectoral girdle show no deviation from the pattern seen in the *S. elegans* group.

I have seen very little of the gill arches, braincase, and other endoskeleton and will not attempt to describe them.

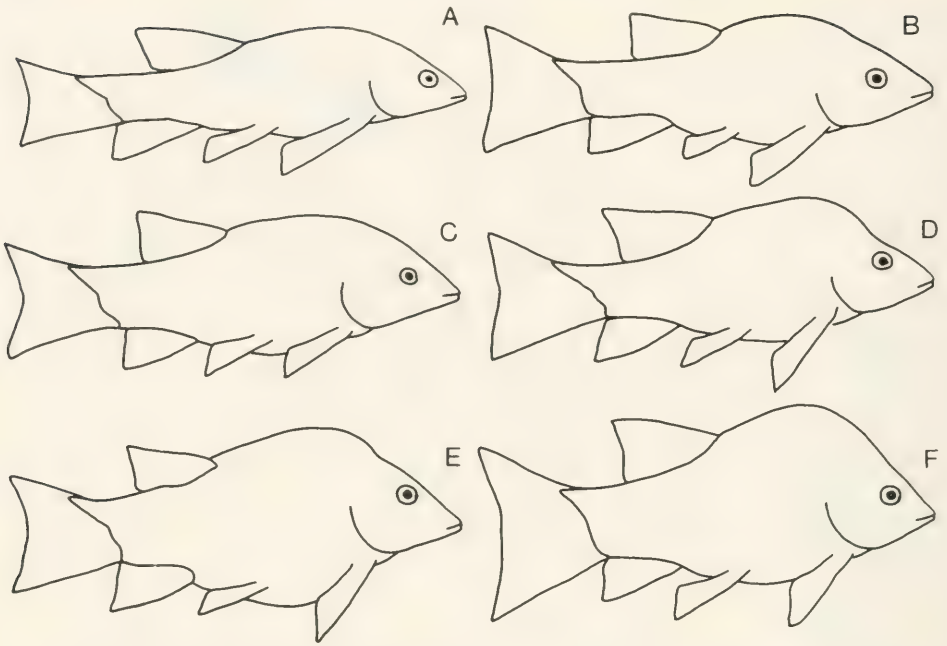


FIG. 27. Variation in body shape of species in the *S. tenuiceps* group. Outline drawings based on complete specimens, in most cases the holotype. A, *S. greenwoodi* YPM 8970; B, *S. decoratus* YPM 8957; C, *S. fundus* YPM 8927; D, *S. tenuiceps* YPM 8162; E, *S. saginatus* YPM 8932. F, *S. profundus* YPM 8944.

Body Shape

The several species in the *S. tenuiceps* group described here vary substantially in body shape (Fig. 27), from slender to very deep bodied, ranging in body depth from about 26–52% of standard length. The slope of the forehead relative to horizontal is 30–50° but usually less than 40°. Some species have a pronounced dorsal hump directly behind the head, whereas in others the outline of the back curves gently from the skull to the dorsal fin. Head length is somewhat variable over all species (27–35% of standard length), but most are in the range of about 30–35% of standard length. Caudal peduncle depth tends to be variable (25–54% of DFCD), and correlated with body depth. Of the fish measured, primarily from the Towaco Formation of the Newark Basin in New Jersey, the maximum size is about 17 cm standard length. These data are summarized in Table 25.

Squamation

Species in the *S. tenuiceps* complex are completely covered by a fabric of interlocking rhomboid scales with smooth posterior margins. The scales are generally largest anteriorly near the lateral line. They decrease in size ventrally, caudally, and dorsally. In some species, for example *Semionotus fundus* and *Semionotus decoratus*, there may be intercalated scale rows in the epaxial region anterior to the dorsal fin. Unlike the intercalary scale rows in macrosemiids described by Bartram (1977), these extra scale rows are not intraspecifically consistent nor is the pattern the same on both sides of the same individual. They are, however, more common in some species than others. The lateral line is complete and relatively straight and passes through midflank. Lateral line scales number 32–36. The median scales on the caudal peduncle are enlarged relative to the lateral caudal scales. These scales are in linear series with the paired fulcra fringing the caudal fin. Both the dorsal and anal fins are preceded by a large oval scale, which

Table 25. Summary of morphometric data for the *Semionotus tenuiceps* group. MAXCD** = MAXCD x 100/DFCD. MAXCD* = MAXCD x 100/AFCD. All other variables expressed as % SL, for SL = 7.4 to 16.8 cm.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
DPTH	22	40.06	7.49	26.72	52.38
HDL	20	31.36	2.26	26.60	34.65
PDL	20	64.96	3.46	59.22	70.65
DFFV	20	32.82	6.23	22.41	42.55
DFAN	20	31.61	4.78	21.82	40.43
DFCD	22	42.29	2.64	36.90	47.57
AFCD	20	28.50	1.89	24.14	32.10
HDD	22	27.22	3.73	19.66	34.52
MAXCD	21	17.57	3.51	10.91	23.81
MINCD	22	15.30	2.68	10.91	20.24
PTAL	20	47.03	1.97	44.14	50.42
DFPT	22	44.17	5.04	36.03	52.78
DFB	15	16.57	2.30	12.82	20.59
AFB	18	10.43	1.48	7.76	13.51
MAXCD**	29	42.30	7.64	25.00	54.05
MAXCD*	28	61.74	9.84	35.29	80.95

is about twice the length of an ordinary flank scale. The predorsal scale abuts the first fulcrum of the dorsal fin, and the fin itself originates between the 19th and 21st vertical scale row, and 9–12 scales above the lateral line. The enlarged preanal scale lies a bit in front of the anal fin and vent. The anal fin originates behind the 17th to 19th vertical scale row, but usually two rows in front of the dorsal fin and from 9–12 scales below the lateral line. The pelvic fins originate behind rows 7–9.

Fins

All fins are fringed by fulcra and are composed of paired lepidotrichia that are unsegmented at their bases and segmented distally. The ends of the segmented rays are difficult to see in most specimens because they branch at least 2 times and feather out toward their tips, but they always extend beyond the last fringing fulcrum. The length of the dorsal and anal fin bases is about 14–19% and 9–12% of standard length, respectively. Although the dorsal fin originates about 2 scale rows behind the anal fin, it is placed slightly in front of the anal in lateral view. In both the dorsal and anal fins, there is a single unpaired basal fulcrum, two paired basal fulcra, and up to nine paired fringing fulcra, of which two or three lie against the basal unsegmented portion of the first lepidotrichium. Lepidotrichia number 7 to 9 in both fins.

The pectoral fins have up to 17 lepidotrichia and are fringed by about 7 fulcra. The pelvic fins, originating between scale rows 7–9, are composed of 3–5 lepidotrichia and fringed by up to 6 fulcra. There are 15–18 caudal lepidotrichia in the caudal fin. Lepidotrichia dorsal to the lateral line are usually equal in number or greater than lepidotrichia ventral to the lateral line. The most dorsal ray is probably a continuation of the most posterior scale in the axial lobe of the tail (Olsen and McCune ms).

Semionotus tenuiceps Agassiz

Figs. 24, 27, 28, 29, 43; Tables 26, 32

Eurynotes tenuiceps Agassiz (1835)

Paleoniscus latus J. H. Redfield (1837)

Paleoniscus agassiz W. C. Redfield (1841)

Ischypterus latus Egerton (1850)

Ischypterus tenuiceps ceratocephalus Emmons (1857)

Eurinotus ceratocephalus Emmons (1860)

Ischypterus latus Traquair (1877)

Ischypterus tenuiceps Newberry (1888)

Ischypterus latus Newberry (1888)

Semionotus tenuiceps Woodward (1895)

Type locality. Whitmore's Ferry, Sunderland, Massachusetts

Collector. Edward Hitchcock

Formation. Turner's Falls Sandstone, Deerfield Basin, Massachusetts

Age. Early Jurassic

Holotype. Agassiz did not designate a holotype for "*Eurynotes tenuiceps*" explicitly, but the specimen he figured (Fig. 43) from Murchison's private collection (collected by Edward Hitchcock) has served as the holotype (Woodward 1895). According to Agassiz (1835) and later Woodward (1895), the specimen, which by then had become *S. tenuiceps*, had been deposited in the Geological Society of London (now BGS.GSM) by Murchison. Today, however, there is no record of its ever having been there (the fate of a fair portion of Murchison's collection is unknown (Andrews 1982)). Without success, I have searched for Agassiz's figured specimen of *Semionotus* (= *Eurynotes*) *tenuiceps* at the Geological Society of London, the British Museum (Natural History), the Institut de Géologie de l'Université de Neuchâtel, the Museum of Comparative Zoology, and the Pratt Museum, Amherst College (which holds Hitchcock's collection). In addition, I have examined Agassiz's notes and the manuscript for *Recherches sur les Poissons Fossiles* at l'Archiv de l'État in Neuchâtel, as well as selected Agassiz correspondence there and at the Museum of Comparative Zoology and the Houghton libraries of Harvard University for mention of the whereabouts of the specimen. The holotype of *S. tenuiceps* must be considered lost. No syntypes are available, as Agassiz used only the holotype for his description. Therefore, I designate a neotype specimen to serve as the standard of comparison for *S. tenuiceps* (see below).

Neotype. YPM 8162 (Fig. 43; see also fig. 11b in Olsen and others 1982) complete specimen, negatively prepared, counterpart unknown

Collector. Unknown, possibly J. H. Redfield

Neotype locality. Whitmore's Ferry, Sunderland, Massachusetts

Formation. Lower Turner's Falls Sandstone

Age. Hettangian, Early Jurassic

Neoparatypes. YPM (all from the P4 excavation) 8921, 8945, 8946, 8947, 8948, 8949, 8950, 8961, 8972, 8981

Diagnosis. A moderately deep-bodied *Semionotus* with a pronounced dorsal hump and very large helmet-shaped scales along the dorsal midline. Relative to others in the *S. tenuiceps* group, this species is deeper bodied than *Semionotus greenwoodi*, *S. fundus*, and *S. decoratus* but more slender than *S. saginatus* and *Semionotus profundus* (all described below; Fig. 27). *S. tenuiceps* is distinguished from the species most similar in body form, *S. fundus*, by its pronounced dorsal hump and robust anterior dorsal ridge scales. The largest dorsal ridge scales begin two to

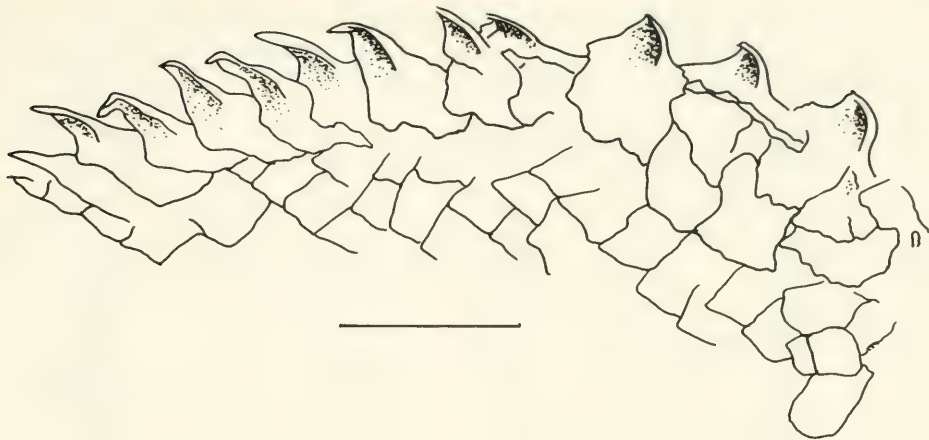


FIG. 28. *S. tenuiceps* dorsal ridge scales from YPM 8162.

three scales posterior to the extrascapulars rather than at about the sixth scale behind the extrascapulars, as is the case in *S. greenwoodi*, *S. fundus*, and *S. saginatus*.

Distribution. Sunderland, Massachusetts, and Turner's Falls, Massachusetts, in the Deerfield Basin, Hettangian; Pompton (and probably Martinsville and East Round Top), New Jersey, in the Newark Basin, Hettangian; Haymarket, Virginia, in the Culpeper Basin (Hentz 1981), Sinemurian.

Description. The neotype of *S. tenuiceps* has well-preserved robust dorsal ridge scales (Fig. 28; Olsen and others 1982). The first two scales behind the extrascapulars are unmodified. The next three are very large helmet-shaped scales (Fig. 28) that expand basally along an anterior-posterior axis. The ganoine-covered spines point first dorsally and then curve posteriorly. Except for its very tip, the spine is not a free-standing extension of the scale base; rather, it has the appearance of being elevated dorsally by a large mass of bone not covered by ganoine. From about the 6th to 12th dorsal ridge scale, the scale base is reduced in size. The spines still point in a dorsoposterior direction, but more posteriorly and less dorsally than the large helmet-shaped scales in front of them. The most posterior scales are simple, convex, and have spines extending beyond the scale base and overlapping the scale behind it in the series. The total number of dorsal ridge scales is about 19, including the predorsal scale.

S. tenuiceps is relatively deep bodied, with a pronounced dorsal hump and a deep belly (Fig. 29D). The forehead slopes at about 30–40° relative to horizontal. The caudal peduncle is narrow relative to *S. profundus* and *S. saginatus* and narrows more rapidly from the dorsal and anal fins toward the caudal fin than does *S. profundus*. The species most similar in body shape to *S. tenuiceps* are easily distinguished by their globular dorsal ridge scales, and they also differ slightly in body shape. Figure 29 (C, D) illustrates the difference in body shape between *S. tenuiceps* and *S. fundus* as well as *S. saginatus*, while taking into account intraspecific variability by showing a scatter plot of the distribution of fin positions. Morphometric data are summarized in Table 26. A caveat is necessary at this point: In compliance with Art. 75c-5 (ICZN 1964), the neotype of *S. tenuiceps* is a specimen from Sunderland in the Deerfield Basin. However, the neoparatypes are all from the Newark Basin. The body depth relative to standard length for the neotype is on the high side of the range for body depth among the neoparatypes from the Newark Basin. With more specimens, the depth-to-length ratio might

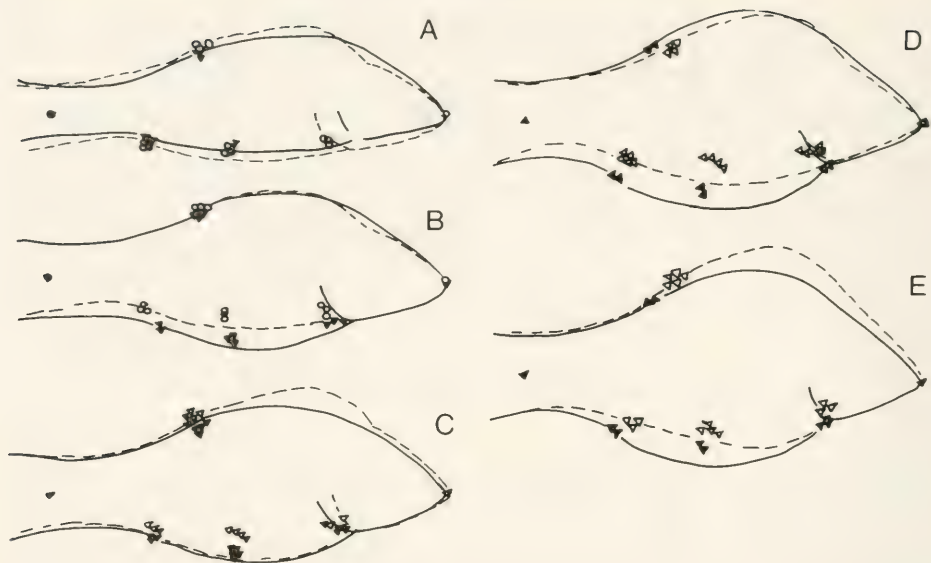


FIG. 29. Comparisons of body shape, *S. tenuiceps* group. For each comparison, the species that corresponds to the solid line and solid symbol is given first. A, *S. greenwoodi* versus *S. decoratus*; B, *S. fundus* versus *S. decoratus*; C, *S. fundus* versus *S. tenuiceps*; D, *S. saginatus* versus *S. tenuiceps*; E, *S. saginatus* versus *S. profundus*.

actually be bimodal or trimodal, and *S. tenuiceps* as described here could include two species. Given the geographic and stratigraphic limitations of this work, uncertainty is unavoidable.

Flank scales covering the anterior portion of the body and near the lateral line are the largest. Caudally, dorsally and ventrally, the scales decrease in size. On the neotype, some of the scales in the predorsal region dorsal to the lateral line were lost in preservation, but on the area remaining there are no intercalary scale rows. Extra rows do occur rarely in *S. tenuiceps* from the Yale P4 excavation in Pompton, New Jersey (for example YPM 8949). However, as some semionotids have different numbers of intercalary scale rows on the left and right side of the same fish (Olsen and McCune ms), the presence of intercalary rows is not taxonomically significant at the species level (which does not preclude ecological significance between localities or the significance of a developmental tendency to produce extra scale rows that is statistically demonstrable at some higher taxonomic level).

Lateral line scales number 33–36, usually about 34. There are nine vertical scale rows anterior to the pelvic fin, 18–19 to the anal fin, and 21 to the dorsal fin. Between the 21st lateral line scale and the dorsal fin there are 10 scales. Below the lateral line, there are 9 scales to the origin of the anal fin.

The dorsal fin has 10–12 rays and is fringed by about 9 fulcra. The first three are basal fulcra, the next three lie against the unsegmented portion of the first ray, and the remaining three or more fringe the segmented portion of the first lepidotrichium. Anal rays number 7–10. On the anal fin there are three basal fulcra and about 6 fringing fulcra, 3 of which fringe the unsegmented lepidotrichium base. The best view of a pectoral fin (YPM 8948) shows 17 lepidotrichia and about 7 fulcra. The pelvic fins on this same specimen appear to have 5 rays fringed with 6 fulcra. When appressed to the body, the tips of the pectoral fins reach the origin of the pelvic fins, and the pelvic fins extend as far as the preanal scale.

Table 26. Summary of morphometric data for *Semionotus tenuiceps*.
 $\text{MAXCD}^* = \text{MAXCD} \times 100/\text{DFCD}$. $\text{MAXCD}^{**} = \text{MAXCD} \times 100/\text{AFCD}$. All other
variables expressed as % SL, for SL = 10.1 to 16.8 cm.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
DPTH	4	39.18	3.62	36.21	44.05
HDL	4	32.31	1.84	30.36	34.65
PDL	3	66.61	1.72	64.66	67.86
DFPV	3	32.30	2.59	29.31	33.93
DFAN	4	30.97	0.94	29.63	31.68
DFCD	4	41.08	2.79	36.90	42.59
AFCD	4	27.78	0.82	26.72	28.70
HDD	4	27.29	1.79	25.00	28.71
MAXCD	4	16.88	1.47	15.52	18.45
MINCD	4	14.60	0.96	13.79	15.84
PTAL	4	47.48	1.41	45.54	48.81
DFPT	4	43.05	3.16	40.59	47.62
DFB	4	15.94	2.13	13.10	18.10
RAFB	4	10.05	0.63	9.21	10.71
MAXCD*	9	42.24	5.16	35.42	50.00
MAXCD**	9	60.89	3.53	54.84	65.96

Good skull material is limited. YPM 8162 affords a particularly good view of a reasonably complete articulated skull (Fig. 25). See the description (above) or the description of the *S. elegans* group (Olsen and McCune ms).

Semionotus greenwoodi, new species

Figs. 27, 29, 30, 44; Tables 27, 32

Diagnosis. *S. greenwoodi* is distinguished from all other species of the *S. tenuiceps* group by its very slender body form, short head, and smoothly sloping profile from the nape onto the skull roof. The slender body form of *S. greenwoodi* relative to all others is reflected quantitatively by the values of eight linear measurements, taken as percentages of standard length. The values of all these ratios are smaller than corresponding ratios for all other species of the *S. tenuiceps* group. Except for head length (HDL), all measurements (DFPT, DFPV, HDD, MINCD, MAXCD, DPTH, DFAN) are highly correlated with body depth and also related to fin position along the anterior-posterior axis.

The largest dorsal ridge scales of this species are similar to those of *S. fundus* and *S. sarginatus* and not as large as *S. tenuiceps*, *S. decoratus*, or *S. profundus*.

Holotype. YPM 8970 (P4-2180) complete fish, mechanically prepared; counterpart is a negative impression (Fig. 44)

Paratypes. YPM 6586, 8959, 8960, 8967, 8968, 8969, 8971, 8972, 8973, 8974, 8976, 8977

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. Named for P. H. Greenwood, in honor of his outstanding contributions to the study of the species flocks of cichlid fishes living in the African rift lakes

Description. The dorsal ridge scales of *S. greenwoodi* are large relative to the flank scales, as in *S. tenuiceps*, but the largest scales in the series are more posterior

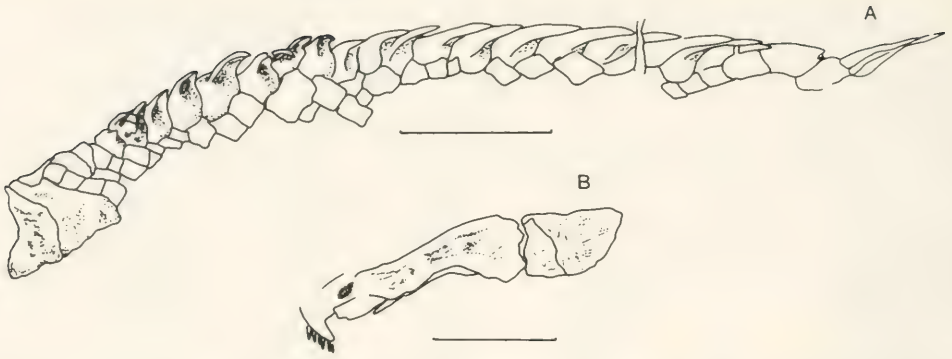


FIG. 30. *S. greenwoodi*. A, dorsal ridge scales of *S. greenwoodi*, holotype YPM 8970; B, frontals and parietals of YPM 8970. Scale = 1 cm.

than they are in *S. tenuiceps* (Fig. 30). The first 3 scales lack spines completely, and the 4th and 5th scales have very broad, short spines. The 6th through 12th scales have large spines and bulbous bases, with only the spines covered by ganoine. Posterior to the 12th dorsal ridge scale, the scale bases become more rounded and flattened with very prominent long spines, very much like the posterior scales of the *S. micropterus* group (Olsen and others 1982). The last scale in the series is a large oval plate that abuts the first unpaired fulcrum on the leading edge of the dorsal fin. The total number of scales in the dorsal series, including the predorsal scale, is about 22.

This species is the most slender and streamlined of the *S. tenuiceps* group. The head is small relative to others in the *S. tenuiceps* group, and the slope of its forehead with respect to horizontal is about 30–40°. Overall body form is most clearly seen by comparison of outline drawings (Fig. 27) of each of the six species in this genus. By visual inspection or by superimposing a tracing of *S. greenwoodi* on outlines of the other species (all at the same standard length), one can easily see that *S. greenwoodi* is more slender than any other species (Fig. 29). These morphometric data are summarized in Table 27.

There are 33 or 34 (usually 34) lateral line scales. The pelvic fin originates at the 8th or 9th (usually 9th) scale row, the dorsal fin at row 20 or 21, and the anal fin at row 18 or 19. The scales along the dorsal and ventral midline of the caudal peduncle are enlarged. Rarely, there are intercalated scale rows dorsal to the lateral line and anterior to the dorsal fin. The scales are largest in the anterior flank region and around the lateral line. They decrease in size both caudally and anterodorsally. From the lateral line, there are 8 scales to the dorsal fin and about 9 to the origin of the anal fin.

The dorsal and anal fins are fringed with 7–9 fulcra; the first 3 are basal fulcra; the bases of the next 2 lie against the unsegmented portion of the first lepidotrichium. There are about 7–11 dorsal and 7–8 anal lepidotrichia. The pectoral and pelvic fins are fringed by at least 6 fulcra. Pelvic lepidotrichia number 3–4, and pectoral lepidotrichia number about 11. In all fins, the tips of the lepidotrichia extend beyond the tip of the last fin fulcrum. The holotype shows all of the fins well except the pectorals. The pectoral fins, when appressed to the body, extend almost to the origin of the pelvis (YPM 6568), and the pelvis extend just to the origin of the anal fin. The anal fin in turn extends just beyond the ventral origin of the caudal fin. The posterior margin of the dorsal fin reaches at least to the region where the scales along the dorsal midline of the caudal peduncle begin to enlarge, or about halfway between the dorsal and caudal fins.

Table 27. Summary of morphometric data for *Semionotus greenwoodi*. MAXCD* = MAXCD x 100/DFCD. MAXCD** = MAXCD x 100/AFCD. All other variables expressed as % SL, for SL = 11.0 to 11.7 cm.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
DPTH	3	28.27	1.60	26.72	29.91
HDL	3	28.55	1.48	27.27	30.17
PDL	3	61.48	2.28	60.00	64.10
DFPV	3	23.31	1.29	22.41	24.79
DFAN	3	24.44	2.47	21.82	26.72
DFCD	3	41.73	1.76	40.17	43.64
AFCD	3	27.18	3.44	24.14	30.91
HDD	3	20.42	0.67	19.66	20.91
MAXCD	3	11.93	0.96	10.91	12.82
MINCD	3	11.36	0.54	10.91	11.97
PTAL	3	47.18	2.73	44.55	50.00
RDFPT	3	39.06	1.98	37.07	41.03
RDFB	2	14.60	2.52	12.82	16.38
RAFB	3	8.73	1.34	7.76	10.26
MAXCD*	3	28.69	3.48	25.00	31.91
MAXCD**	3	44.56	8.07	35.29	50.00

The skull does not differ significantly from the *S. elegans* group (Olsen and McCune ms) or from *Semionotus* (McCune 1986). The frontals are narrow anteriorly, with the preorbital portion longer than the posterior portion. The parietals are simple and rectangular (Fig. 30B). The teeth are simple and conical.

Semionotus decoratus, new species

Figs. 27, 29, 31, 44; Tables 28, 32

Diagnosis. Body deeper (about 35% of standard length) than *S. greenwoodi* but more slender than all other species. Head longer than *S. greenwoodi*. Robust scales appear to occur almost immediately behind the extrascapulars, but as the anterior dorsal scales are very tiny, the first robust scale is probably the fourth dorsal scale. In lateral view, the slight hump of the anterior, dorsal portion of the body also distinguishes this species from the two species most similar in body shape, *S. greenwoodi* and *S. fundus*.

Holotype. YPM 8957 (P4-222a); complete fish, mechanically prepared (Fig. 44). I have chosen YPM 8957 as the holotype over YPM 8953, though in many ways the latter is a better specimen. YPM 8953 has been negatively prepared in hydrochloric acid and therefore shows the details of the skull, squamation, and fins especially well. However, the view of the dorsal hump and of the dorsal ridge scales, which are important species-level characters, is superior in YPM 8957.

Paratypes. YPM 8953, 8955, 8956

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. From *decoratus*, meaning adorned, for the elaborate dorsal ridge scales of this species

Description. Superficially, robust scales appear to begin almost immediately posterior to the extrascapulars, but on close inspection the nape region is populated by many tiny scales and the *S. tenuiceps*-type scales do not begin until about the

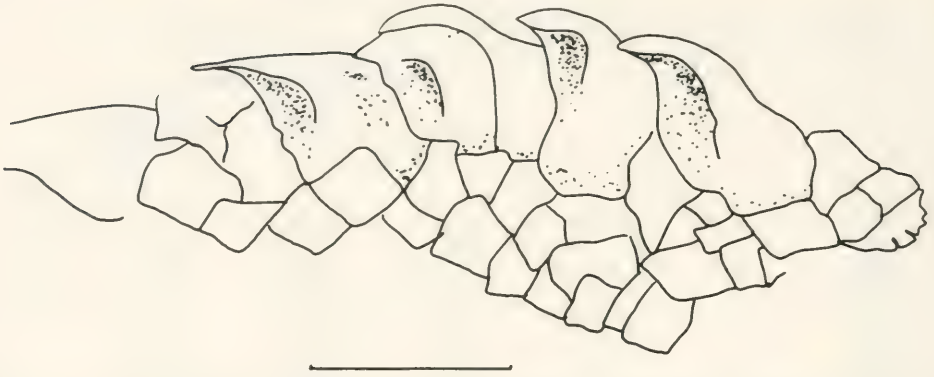


FIG. 31. *S. decoratus*. Dorsal ridge scales of holotype specimen YPM 8957. Scale = 5 mm.

4th scale in the dorsal series (Fig. 31). This position corresponds to the first or second complete vertical scale row behind the cleithrum. There are some (probably 3) incomplete scale rows dorsal to the lateral line and anterior to the first large dorsal ridge scale. Following that there are about 5 robust scales, and then from about scales 11–18 the bases are flat and the elongated spines of each scale overlap the scale behind.

S. decoratus is an ordinary fusiform-shaped fish, with a caudal peduncle that is narrow even close to the anal fin (Fig. 27B). It is slightly deeper bodied than *S. greenwoodi* and more slender than all other species of in the *S. tenuiceps* group. Figure 29 (A, B) illustrates the difference in form of this species relative to *S. greenwoodi* and *S. fundus*. The maximum depth of the caudal peduncle relative to both standard length and tail length is more slender than in all but *S. greenwoodi*. Ratio of head length to standard length is large compared with that of *S. greenwoodi*, and the slope of the forehead is about 30–35° relative to horizontal. Measurements of overall body form are summarized in Table 28.

There are 33–34 lateral line scales. The pelvic fin originates at the 8th–9th scale row, the anal fin originates at row 18–19, and the dorsal fin at row 20–21. The scales along the dorsal and ventral midline of the caudal peduncle are enlarged and form a series with the fulcra fringing the caudal fin. There are frequent intercalated scale rows (9 in YPM 8953) in the area dorsal to the lateral line and anterior to the dorsal fin, especially in the nape region, where the scales are very tiny. The flank scales are largest in the anterior flank region and decrease in size caudally, dorsally and ventrally.

Both the dorsal and anal fins are fringed with 7–9 fulcra, 3 of which are basal fulcra, and two more lie against the unsegmented portion of the first lepidotrichium. At least 5 fulcra fringe the pectoral fin and 4 fulcra fringe the pelvic fin, but these are minimum counts as no specimen of this species has sufficiently well-preserved paired fins to merit such confidence in fulcra counts. There are 9–12 lepidotrichia in the dorsal fin, 7–9 in the anal fin, 3 in the pelvic fins, and about 13 in the pectoral fins. The pectoral fin count is based on only one, albeit very well-preserved, specimen. If this count is correct, the pectoral fin ray count is very different from the usual 17. Dorsal and pectoral fin lengths for the outline drawing (Fig. 27B) are from YPM 8955; caudal, pectoral, and pelvic fin lengths are from YPM 8953.

The skull of the holotype is not informative. However, the detail of the skull of YPM 8953 is excellent. It clearly shows the single suborbital characteristic of *Semionotus* (McCune 1986) and *S. elegans* group (Olsen and McCune ms).

Table 28. Summary of morphometric data for *Semionotus decoratus*. MAXCD* = MAXCD $\times$ 100/DFCD. MAXCD** = MAXCD $\times$ 100/AFCD. All other variables expressed as % SL, for SL = 11.1 to 13.6 cm.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
DPTH	3	34.89	1.40	33.33	36.04
HDL	3	32.52	1.42	30.88	33.33
PDL	3	62.93	2.47	61.26	65.77
DFPV	2	26.83	1.55	25.74	27.93
DFAN	3	29.08	1.40	27.93	30.63
DFCD	3	44.19	0.83	43.38	45.05
AFCD	3	27.69	0.99	27.03	28.83
HDD	3	26.60	1.95	25.23	28.83
MAXCD	3	14.92	1.53	13.24	16.22
MINCD	3	14.38	1.86	12.50	16.22
PTAL	3	44.68	0.47	44.14	45.05
DFPT	3	38.74	2.39	36.03	40.54
DFB	3	18.87	1.74	17.12	20.59
AFB	3	10.58	0.59	9.91	11.03
MAXCD*	3	33.75	3.12	30.51	36.73
MAXCD**	3	53.92	5.72	48.65	60.00

Semionotus fundus, new species

Figs. 27, 29A, 29B, 32, 44; Tables 29, 32

Diagnosis. *S. fundus* is deeper bodied than *S. greenwoodi* and *S. decoratus* and more slender than either *S. profundus* or *S. saginatus* (Figs. 27, 29B, C). This species differs from the two species most similar in shape, *S. decoratus* and *S. tenuiceps*, by having the globular variety of *S. tenuiceps*-type dorsal ridge scales and by lacking the dorsal postcranial hump shared by *S. decoratus*, *S. tenuiceps*, and *S. profundus*. It differs from all other species in the *S. tenuiceps* group by having only 32 lateral line scales.

Holotype. YPM 8926 (P4-1707); complete fish, no counterpart, mechanically prepared (Fig. 44D)

Paratypes. YPM 8925, 8927

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. From *fundus*, meaning foundation, in acknowledgment of funds for this research provided by the National Science Foundation

Description. The dorsal ridge series is the moderate, globular form (Fig. 32). The 5 anterior scales are slightly enlarged and rounded but spineless. Enlarged scales begin about the 5th or 6th scale, and beyond the 10th–12th the scale bases become smaller and flatter. As the scale bases decrease in size posteriorly, the spines elongate and extend far beyond the scale margin, overlapping the scale posterior to it. The total number of dorsal ridge scales, including the predorsal scale, is 19.

The deeper body of this species relative to *S. decoratus* and *S. greenwoodi* is reflected in larger values of DFPV and DFAN relative to standard length (Table 29; Figs. 27, 29B, C). The back slopes gently to the skull roof, with no postcranial dorsal hump, and the slope of the forehead is about 35–40° relative to horizontal.

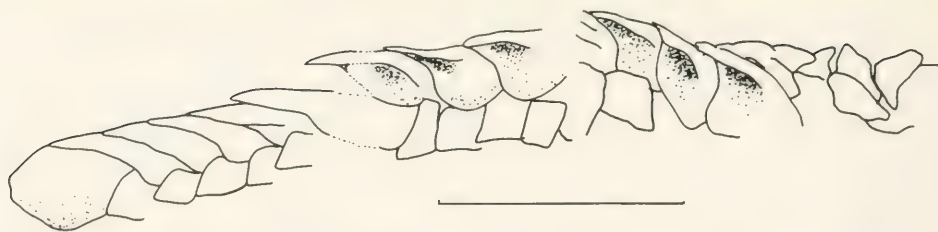


FIG. 32. *S. fundus*. Dorsal ridge scale series of *S. fundus*, holotype YPM 8926. Scale = 1 cm.

The caudal peduncle is deeper anteriorly, and its maximum depth relative to standard length is greater than that of either *S. greenwoodi* or *S. decoratus*.

In all individuals, lateral line scales number 32, fewer than any other species in the *S. tenuiceps* group. There are 7–8 scale rows to the pelvic fins, 17 rows anterior to the anal fin, and 19 rows to the dorsal fin. Between the lateral line and the dorsal fin there are 9 scales; between the lateral line and the anal fin there are 8. As in some other semionotids (Olsen and McCune ms), the pattern of intercalated scale rows is not the same on both sides of the fish. For example, in YPM 8927, there are 9 on one side of the fish and 6 on the other. In addition, the holotype shows the rare instance of intercalated rows ventral to the lateral line. The scales along the ventral and dorsal midline of the caudal peduncle are enlarged. Flank scales are largest in the central anterior flank region and become smaller dorsally, ventrally, and caudally.

The dorsal and anal fins are fringed with about 7–8 fulcra, the first three being basal fulcra and two more lying against the unsegmented portion of the first lepidotrichium. There are about 13 lepidotrichia in the dorsal fin and 10 in the anal fin. The caudal fin consists of 16 lepidotrichia, split equally in number between dorsal and ventral. The pectoral fin consists of 3–4 lepidotrichia, fringed with about 5 fulcra.

The best skull is found on YPM 8927, and it does not differ from other species in the group in any significant respect.

Table 29. Summary of morphometric data for *Semionotus fundus*. MAXCD* = MAXCD x 100/DFCD. MAXCD** = MAXCD x 100/AFCD. All other variables expressed as % SL, for SL = 9.5 to 13.5 cm.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
DPTH	3	38.64	0.87	37.84	39.56
HDL	2	32.25	1.02	31.53	32.97
PDL	2	64.10	3.63	61.54	66.67
DFPV	3	32.34	2.38	29.63	34.07
DFAN	2	31.90	3.07	29.73	34.07
DFCD	3	41.13	1.52	40.00	42.86
AFCD	2	29.15	0.82	28.57	29.73
HDD	3	27.17	3.53	23.70	30.77
MAXCD	2	19.35	0.61	18.92	19.78
MINCD	3	14.44	1.77	13.33	16.48
PTAL	2	45.60	0.78	45.05	46.15
DFPT	3	42.71	1.27	41.76	44.14
DFB	2	15.45	1.46	14.41	16.48
AFB	2	11.00	1.54	9.91	12.09
MAXCD*	2	46.41	0.36	46.15	46.67
MAXCD**	2	66.43	3.96	63.64	69.23

Semionotus profundus, new species

Figs. 27, 29, 33, 44; Tables 30, 32

Diagnosis. *S. profundus* is the most deep-bodied species of the *S. tenuiceps* group. In lateral view, the large dorsal hump posterior to the head and the prominent robust dorsal ridge scales distinguish it from *S. saginatus* (compare Figs. 33 and 34).

Holotype. YPM 8944 (P4-2071); complete fish, part and counterpart, negatively prepared (Fig. 44)

Paratypes. YPM 8913, 8920, 8933, 8934, 8935, 8937, 8938, 8939, 8940, 8941, 8943, 8978

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. From *profundus*, meaning deep, for the gibbose form of this species

Description. *S. profundus* is very deep bodied, with a pronounced dorsal hump (Figs. 27, 44B). The forehead slopes more steeply than in all others in the *S. tenuiceps* group, at about 50° from horizontal, so that the curvature is almost continuous with the anterior descending slope of the dorsal hump. Head depth relative to standard length is greater than in all other species in this group except *S. saginatus*. Maximum depth of the caudal peduncle is also deeper than in all other species, and its outline is almost straight from the dorsal and anal fins to the minimum point of the caudal peduncle, rather than a gently concave curve as in other species. All of these features are most clearly seen in Figures 27 and 29E. Morphometric data are summarized in Table 30.

Commensurate with its deeper body, this species has more horizontal scale rows than other species in the *S. tenuiceps* group except for *S. saginatus*. There are 11 between the lateral line and the dorsal fin and 10–11 between the lateral line and the anal fin, whereas others in the *S. tenuiceps* group have 8–9 scales between the lateral line and either fin. Flank scales are largest anteriorly, near

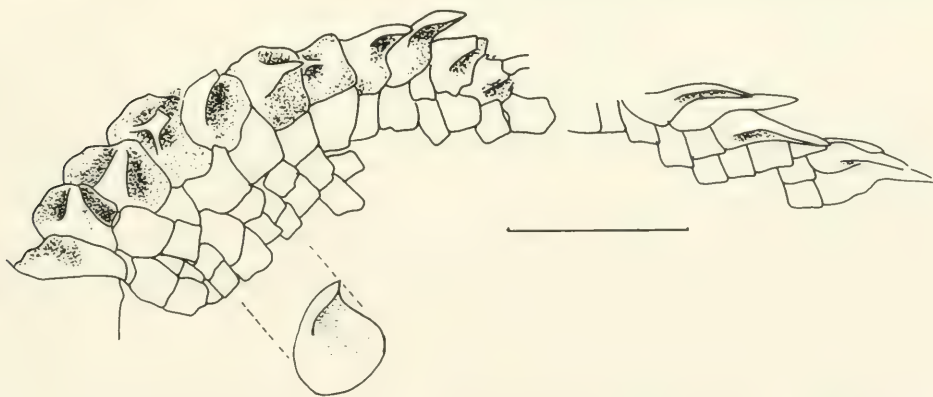


FIG. 33. Dorsal ridge scales of *S. profundus*. Camera lucida drawing. Scale = 1 cm. The scales are pushed to the left side of center, giving a top view on the left side of the fish. This view is somewhat difficult to interpret as the dorsal-ventral height of robust scales is collapsed. However, the base of the scale is clearly expanded along the anterior-posterior axis, and the ganoin-covered spine does not extend much beyond the scale base. Below one of the scales, I give a reconstruction of what I think the scale would look like in side view.

Table 30. Summary of morphometric data for *Semionotus profundus*.
 $\text{MAXCD*} = \text{MAXCD} \times 100/\text{DFCD}$. $\text{MAXCD**} = \text{MAXCD} \times 100/\text{AFCD}$. All other
variables expressed as % SL, for SL = 7.4 to 10.8 cm.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
DPTH	2	48.19	1.26	47.30	49.07
HDL	2	30.82	0.37	30.56	31.08
PDL	2	66.69	2.58	64.86	68.52
DFPV	2	38.58	0.87	37.96	39.19
DFAN	1	39.19	—	39.19	39.19
DFCD	2	43.81	3.03	41.67	45.95
AFCD	1	28.38	—	28.38	28.38
HDD	2	30.36	1.03	29.63	31.08
MAXCD	2	22.13	1.19	21.30	22.97
MINCD	2	18.26	0.94	17.59	18.92
PTAL	1	50.00	—	50.00	50.00
DFPT	2	50.71	2.92	48.65	52.78
DFB	1	17.57	—	17.57	17.57
AFB	1	13.51	—	13.51	13.51
MAXCD*	3	48.60	3.44	44.68	51.11
MAXCD**	2	79.37	2.24	77.78	80.95

the lateral line. They decrease in size caudally, dorsally, and ventrally. On the dorsal flank, anterior to the dorsal fin, there are occasional intercalary scale rows.

Lateral line scales number 33–34. The pelvic fin originates after the 7th–9th vertical scale row, and the anal and dorsal fins originate after rows 17–19 and 19–21, respectively, there being at least one row between them. As in other *Semionotus*, the scales along the dorsal and ventral midline of the caudal peduncle are enlarged.

The dorsal fin of this species is placed a bit forward of that on either *S. fundus* or *S. saginatus*. This fin has 3 basal fulcra and at least 5 fringing fulcra, of which the first two lie against the unsegmented portion of the first ray. Dorsal fin lepidotrichia number about 12. The anal fin also has 3 basal fulcra and at least 5 fringing fulcra, of which two lie against the unsegmented portion of the first ray. The pectoral fins have 17 lepidotrichia and about 7 fringing fulcra. The pelvic fins are composed of 3–4 rays fringed by about 7 fulcra.

The holotype has the best skull of the type series. The frontals are as in other species in the *S. tenuiceps* group, and the teeth are simple and conical.

Semionotus saginatus, new species

Figs. 26, 27, 29, 34, 45; Tables 31, 32

Diagnosis. *S. saginatus* is distinguishable from all other species except *S. profundus* by its deep body. It differs from *S. profundus* in that a greater portion of its depth is distributed below rather than above its lateral line. In addition, it differs from *S. profundus*, *S. tenuiceps*, and *S. decoratus* by having moderate globular scales.

Holotype. YPM 8932 (P4-735); complete fish, part mechanically prepared and counterpart negatively prepared (Fig. 45)

Paratypes. YPM 8928, 8929, 8930, 8931

Type locality. Yale excavation in cycle P4, Pompton, New Jersey

Formation. Towaco Formation, Newark Basin

Age. Hettangian, Early Jurassic

Etymology. From *saginatus*, meaning fattened

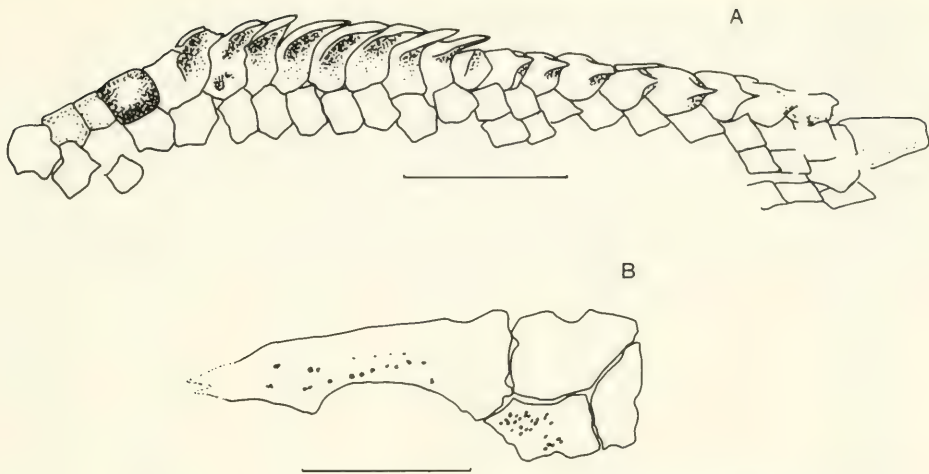


FIG. 34. *S. saginatus*. A, camera lucida drawing of dorsal ridge scales of YPM 8932, holotype; B, camera lucida drawing of frontals, YPM 8929. Scale = 1 cm.

Description. The dorsal ridge scales of *S. saginatus* are globular (Fig. 34). In the holotype, the first 3 dorsal ridge scales are only slightly enlarged, slightly convex, and almost radially symmetrical with no spine. The 4th scale is like the first three but much larger and more convex, radially symmetrical, and lacking a spine. The 5th through 12th scales are large, with bulbous bases and prominent spines covered with ganoine. The spines do not overlap the next scale in the series. Scales 13–20 have flatter, smaller bases and more prominent spines. The 21st scale is the spineless predorsal scale. In most individuals, the posterior 5 scales in the series have spines that look like the anterior scales in the *S. micropterus* group (Olsen and others 1982). At least one spine in the posterior region of YPM 8932 is elongated, and several are definitely short (not broken). Whether the remaining posterior scales are short spined or just broken is ambiguous. If real, the short spines may be an anomalous variation as the spines are prominent on posterior scales in other specimens of *S. saginatus*. The general form of the dorsal ridge scales is similar to those of *S. greenwoodi* and *S. fundus* but less prominent than those of *S. profundus*, *S. tenuiceps*, and *S. decoratus*.

S. saginatus is deeper bodied than all but *S. profundus*, but in the former, a greater proportion of this body depth is ventral to the lateral line (Figs. 27, 29D, E). The slope of the skull roof is about 35–40° relative to horizontal. The dorsal fin is more posteriorly placed than in *S. profundus*. Morphometric data are summarized in Table 31.

There are 33–35 lateral line scales. The pelvic, anal, and dorsal fin positions are at rows 7–9, 17–19, and about 21, respectively. There are about 11 scales between the lateral line and the dorsal fin and 10–12 below the lateral line at the anal fin. Scale size decreases dorsally, ventrally, and caudally. There do not seem to be any intercalary scale rows on the flank, although this tendency is so variable in other species that their apparent absence may not be significant.

The dorsal fin is preceded by 3 basal fulcra and fringed with about 5 more. Three of the fringing fulcra lie against the unsegmented portion of the first fin ray. The rays or lepidotrichia number 10–11 in the dorsal fin and about 9 in the anal fin. Like the dorsal fin, the anal fin is preceded by 3 basal fulcra and fringed with 5 more, two of which lie against the unsegmented portion of the first lepidotrichium. The pectoral fin comprises about 16 lepidotrichia and is fringed

Table 31. Summary of morphometric data for *Semionotus saginatus*.
 $\text{MAXCD*} = \text{MAXCD} \times 100/\text{DFCD}$. $\text{MAXCD**} = \text{MAXCD} \times 100/\text{AFCD}$. All other
 variables expressed as % SL, for SL = 10.8 to 11.9 cm.

Variable	N	Mean	Standard deviation	Minimum value	Maximum value
DPTH	2	46.55	4.29	43.52	49.58
HDL	2	33.52	1.05	32.77	34.26
PDL	2	69.55	1.46	68.52	70.59
DFPV	2	38.73	1.08	37.96	39.50
DFAN	2	31.66	1.57	30.56	32.77
DFCD	2	38.35	0.76	37.82	38.89
AFCD	2	27.71	1.22	26.85	28.57
HDD	2	29.94	0.44	29.63	30.25
MAXCD	2	18.46	1.23	17.59	19.33
MINCD	2	16.23	2.00	14.81	17.65
PTAL	2	49.75	0.95	49.07	50.42
DFPT	2	49.79	0.30	49.58	50.00
DFB	1	13.45	—	13.45	13.45
AFB	2	9.63	1.83	8.33	10.92
MAXCD*	2	48.37	3.42	43.48	54.05
MAXCD**	2	70.55	8.18	57.14	80.95

by an undetermined number of fulcra. The pelvics, as in other species of the *S. tenuiceps* group, have about 4 rays, and again the number of fulcra is not visible. The caudal fin has 8 rays ventrally and 8–9 dorsally.

The skull is very well preserved in the holotype (Fig. 26) and shows nothing unusual for this group. One of the paratypes (YPM 8929) shows the frontals particularly well (Fig. 34). As in other Newark semionotids, the teeth are simple and conical.

7. PATTERNS OF VARIATION

Most of the observed variation in semionotids is confined to two complexes of characters—dorsal ridge scales and body shape. Although a few other characters, such as the shape of the caudal fin or the number of lateral line scales, are variable, only a few species deviate from the common condition for these characters. These rarely varying characters, which have little more taxonomic value than in the definition of particular species, are reviewed below, followed by a discussion of the more variable characters, body shape, and morphology of the dorsal ridge scales.

FINS AND FLANK SCALES

Data for *Semionotus* from cycle P4 and Europe are summarized in Table 32. The ranges of variability for meristic characters overlap in most species. Only a few species have ranges for a given variable that are outside the range of all or most other species. For example, *S. amplicephalus* has 13–14 vertical scale rows anterior to the insertion of the pelvic fin and only 30 lateral line scales, whereas the total range of variation in these variables for all other species is 7–11 and 31–40, respectively. This case is notable because the two scale counts are skewed in opposite directions: the pelvic count is high but the lateral line count is low.

The number of horizontal scale rows (from dorsal fin to lateral line and from anal fin to lateral line) is usually high in deep-bodied species such as *S. schaefferi*, *S. latheticus*, *S. convalis*, *S. minor*, *S. profundus*, and *S. saginatus* and low in slender species such as *S. kirschi* and *S. johberryi*. Similarly, the slope of the forehead in deep-bodied species (*S. schaefferi*, *S. olseni*, *S. minor*, *S. convalis*, *S. profundus*) is usually higher than it is in slender-bodied species (*S. kirschi*, *S. anosteus*, *S. johberryi*). To some degree, both the slope of the forehead and number of horizontal scale rows are subsumed by the character body shape (see below). The fact that deep- and slender-bodied fish have differing scale counts independently supports the arguments made earlier that distortion does not account for the variation in body shape.

The number of lateral line scales characteristic of *S. kapffi* overlaps the ranges of only two other species, *S. euthenius* and *S. thomsoni* (aside from the anomalous *S. amplicephalus*). In the latter two species, the mean number of lateral line scales is higher than in *S. kapffi* (34.6 and 34.5 versus 32).

Although the shape of the caudal fin is not easily determined in many cases, it is forked in *S. virginiae* and *S. thomsoni* but only weakly emarginate in all other species when it is clearly visible.

The range of variation in number of lepidotrichia and fulcra is the same in a given fin for all species. The only exceptions are the fin fulcra of two European species, *S. bergeri* and *S. normanniae*. In these two species, there are more basal fin fulcra, more fulcra lying against the unsegmented portion of the first lepidotrichium, and more fulcra altogether on the dorsal fin (and probably the anal fin) than on any semionotid from P4. Unfortunately, the number of specimens of European species on which this statement is based is small, particularly in the case of *S. normanniae*. *S. minor* presents an intermediate case. It has an unusually high number of basal fulcra on the dorsal fin (five rather than three to four, usually three), but it also has the five additional long, slender, fringing fulcra seen in all Newark semionotids discussed here.

Intercalated scale rows in the epaxial region anterior to the dorsal fin are

Table 32. Summary of Morphological Data for *Semionotus* from Europe and from Towaco cycle P4

Species	Scales						
	drs	plvsc	anfsc	dfsc	cdsc	vdsc	vvsc
<i>S. bergeri</i>	-	11-11	17-21	20-24	34-37	-	-
<i>S. kapfji</i>	-	-	18-22	21-23	32-33	-	-
<i>S. normanniae</i>	-	-	-	21-21	-	-	-
<i>S. minor</i>	22-22	9-10	19-20	21-24	35-38	10-11	8-12
<i>S. kirschi</i>	19-19	8-11	18-22	20-24	33-39	7-8	8-8
<i>S. olseni</i>	20-20	8-10	17-19	18-22	33-37	9-11	9-9
<i>S. virginiae</i>	18-19	7-10	17-21	18-26	33-40	7-10	7-11
<i>S. thomsoni</i>	20-20	7-10	16-20	19-22	31-36	8-10	7-10
<i>S. convalis</i>	18-18	9-9	17-17	20-20	36-36	11-11	11-11
<i>S. redfieldii</i>	19-19	7-10	17-20	19-24	33-37	9-11	8-10
<i>S. eutheniuss</i>	20-20	7-10	16-21	19-24	32-38	8-12	7-11
<i>S. schaefferi</i>	18-18	7-9	16-20	18-23	33-37	10-13	10-12
<i>S. latheticus</i>	20-20	8-8	17-17	19-19	34-34	13-13	10-10
<i>S. melanimus</i>	21-21	-	21-21	24-24	38-38	-	-
<i>S. anosteus</i>	19-19	7-7	19-19	21-21	33-33	9-10	9-9
<i>S. johberyi</i>	21-21	-	20-20	21-21	34-34	8-8	7-7
<i>S. amplicephalus</i>	-	13-14	-	-	30-30	-	-
<i>S. tenuiceps</i>	19-19	9-9	18-19	21-21	33-36	10-10	9-9
<i>S. greenwoodi</i>	22-22	8-9	18-19	20-21	34-34	8-8	9-9
<i>S. decoratus</i>	19-19	9-9	18-19	20-21	33-34	9-9	8-8
<i>S. fundus</i>	19-19	7-8	17-17	19-19	32-32	8-8	8-8
<i>S. profundus</i>	21-21	7-9	17-19	19-21	33-34	11-11	10-11
<i>S. saginatus</i>	21-21	7-9	17-19	21-21	33-35	12-12	12-12

Continued on next page

difficult to interpret. Bartram (1977) believed that the presence of these extra scale rows was a synapomorphy of the Macrosemidae, the sister group to the Semionotidae (Olsen and McCune ms). However, in many species of semionotids from P4 and also in the *S. elegans* group, the occurrence of these extra scale rows is not only variable within species but may differ on the right and left sides of the same individual. Most semionotids with intercalary scale rows have only a few extra rows, but one individual has as many as nine extra rows (*S. decoratus*, YPM 8957), and in two individuals, the predorsal scales above the lateral line are completely doubled [*Semionotus* sp. (YPM 8846) from P4, and *Semionotus* sp. (AMNH 3210) from Sunderland, Massachusetts]. Therefore, neither the presence nor frequency of intercalary scale rows is useful for relating species within the family. Paradoxically, though the presence of intercalary scale rows is often not consistent on both sides of the same individual, the tendency to produce these scale rows could be considered a synapomorphy uniting macrosemiids and semionotids (as variants indicating a higher level homology sensu Roth (1984) of the developmental pathway that produces scales).

DORSAL RIDGE SCALES

One of the more prominent fields of variability in Newark semionotids is the morphology of the dorsal ridge scale series. Seven morphologies of dorsal ridge scales are exhibited by semionotids from cycle P4 (Fig. 9). These have been described in detail on pages 30-34. In all types, the morphology of individual scales changes with position along the anterior-posterior axis of the series. The anterior scales in each series are always most distinctive, allowing definite identification of dorsal ridge scale type on the basis of these anterior scales alone. Modified simple, small, thin-spined, and concave scales (Fig. 9B, C, D, G) can

Table 32--continued

Species	fh	cf	is	drst	Fin fulcra					
					dff1	dff2	dff3	aff1	aff2	aff3
<i>S. bergeri</i>	30-40	-	-	s	4-6	10-10	15-15	-	-	14-14
<i>S. kapffii</i>	-	-	-	s	4-4	7-7	-	-	-	-
<i>S. normanniae</i>	-	-	-	s	5-5	>8	-	-	-	-
<i>S. minor</i>	50-50	-	-	s-ms	5-5	6-7	>10	3-3	5-5	>7
<i>S. kirschi</i>	15-25	we	rare	s	3-4	4-5	6-8	3-3	5-6	6-7
<i>S. olseni</i>	50-60	we	none	s	3-4	5-5	7-8	3-3	6-6	8-8
<i>S. virginiae</i>	35-40	f	rare	s	3-4	4-6	6-8	2-3	4-5	6-8
<i>S. thomsoni</i>	30-40	f	occ	s	3-4	4-6	5-8	2-3	4-5	6-9
<i>S. convalis</i>	50-50	-	none	s	3-3	-	6-6	3-3	5-5	8-8
<i>S. redfieldii</i>	35-40	we	none	s	3-4	5-6	7-8	2-4	5-6	6-8
<i>S. euthenius</i>	40-50	we	occ	s	3-4	4-6	5-8	2-3	4-5	5-9
<i>S. schaefferi</i>	50-65	we	occ	ms	3-4	4-6	6-8	3-3	5-5	7-9
<i>S. latheticus</i>	45-45	-	-	m	3-3	5-5	-	-	-	-
<i>S. melanimus</i>	35-35	-	occ	m	3-3	5-5	8-8	3-3	-	7-7
<i>S. anosteus</i>	30-30	-	none	ms	3-3	5-6	7-8	3-3	5-5	8-10
<i>S. johberryi</i>	30-30	-	occ	ms	-	-	-	-	-	7-7
<i>S. amplicephalus</i>	-	-	-	ms	-	-	-	-	-	-
<i>S. tenuiceps</i>	30-40	we	none	r	3-4	5-6	8-11	3-3	5-6	9-12
<i>S. greenwoodi</i>	30-40	we	rare	g	3-3	5-6	7-7	3-3	5-5	7-7
<i>S. decoratus</i>	30-35	we	freq	r	3-3	5-5	7-9	3-3	5-5	7-9
<i>S. fundus</i>	35-40	we	occ	g	3-3	5-5	7-7	3-3	5-5	8-8
<i>S. profundus</i>	50-50	we	occ	r	3-3	7-7	8-8	-	-	9-9
<i>S. saginatus</i>	35-40	we	rare	g	3-3	6-6	8-8	-	5-5	-

Abbreviations: cf=caudal fin shape (we=weakly emarginate, f=forked), drst=dorsal ridge scale type (c=concave, g=globular, r=robust, ms=modified simple, s=simple, sm=small, t=thin-spined), fh=angle of forehead in degrees from horizontal, is=intercalated scales (none, rare, occasional, frequent).

Continued on next page

be recognized with reasonable confidence on the basis of posterior scales. Simple, globular, and robust scales (Fig. 9A, E, F) cannot be identified from only the posterior scales in the series. Different dorsal ridge scale morphologies cannot be accounted for by ontogenetic change, because the size range of fishes having different dorsal ridge scale types is comparable (most between 7 and 12 cm). There are no very small individuals (less than 5 cm) in which very early stages of dorsal ridge scale development can be seen, but in very large individuals the morphology of individual scales is no different from that of smaller individuals.

In addition to the types of dorsal ridge scales previously described, there are occasional anomalous variants on these themes. Rarely, a dorsal ridge scale series of one type will include one or a few "sports" of another type (Fig. 35). Another kind of variant involves the doubling or tripling of scales in the dorsal ridge series (Fig. 35). Several variants involve doublings of only one or two scales in the series (Fig. 35C, G, M) although in a few a large portion of the series is doubled (Fig. 35A, B, D, F) or tripled (Fig. 35E). Most specimens showing dorsal ridge scale anomalies are incomplete and therefore indeterminate at the species level, but supernumerary dorsal ridge scales do not seem to be characteristic of a particular species. There are supernumerary scales in concave (Fig. 35M), modified simple (Fig. 35B), simple (Fig. 35A), and globular (Fig. 35D) dorsal ridge scale series. There are also at least two cases of double dorsal ridge scales in *S. capensis* from South Africa (Fig. 35E).

The generation of scale doublings may occur in several ways. One specimen has a hoof-shaped dorsal scale (Fig. 35I), suggesting that the rudiment of the median dorsal ridge scale is producing two scales. In some individuals with concave scales, the scales lateral to the dorsal ridge scale series develop spines (Fig. 35G,

Table 32--continued

Species	Fin fulcra		Fin rays					
	pctf	plvf	dors	anal	pct	plv	cddr	cdvr
<i>S. bergeri</i>	-	-	13-15	7-10	-	4-4	8-8	8-9
<i>S. kapffi</i>	-	-	-	-	-	-	-	-
<i>S. normanniae</i>	>17	-	-	-	>13	-	10-10	7-7
<i>S. minor</i>	9-9	>4	12-12	10-10	17-17	4-7	10-10	8-8
<i>S. kirschi</i>	5-7	6-7	9-14	8-10	11-16	3-5	7-9	8-8
<i>S. olseni</i>	10-10	5-8	12-12	10	15-15	5-5	-	8-8
<i>S. virginiae</i>	5-7	4-6	9-12	8-11	15-17	3-6	9-9	8-8
<i>S. thomsoni</i>	5-7	4-6	10-13	8-10	13-16	3-6	9-9	8-8
<i>S. convalis</i>	6-6	4-4	13-13	9-9	13-13	5-5	9-9	8-8
<i>S. redfieldii</i>	-	5-5	10-12	9-10	-	3-7	9-9	8-9
<i>S. eulhenius</i>	5-7	5-8	10-13	8-12	14-17	3-8	8-9	8-8
<i>S. schaefferi</i>	6-7	6-6	10-12	8-11	17-17	4-4	8-9	8-9
<i>S. latheticus</i>	-	6-6	-	-	-	3-3	-	8-8
<i>S. melanimus</i>	-	-	11-11	10-10	14-14	-	10-10	9-9
<i>S. anosteus</i>	9-9	6-6	13-13	13-13	-	-	9-9	8-8
<i>S. johberryi</i>	-	-	10-10	15-15	-	-	9-9	9-9
<i>S. amplicephalus</i>	-	-	-	-	-	-	-	-
<i>S. tenuiceps</i>	>7	6-6	10-12	7-10	17-17	5-5	8-9	8-9
<i>S. greenwoodi</i>	6-6	6-6	11-11	8-8	-	-	8-8	7-7
<i>S. decoratus</i>	5-5	4-4	10-12	7-9	-	-	-	-
<i>S. fundus</i>	7-7	-	11-13	9-10	17-17	3-4	8-8	8-8
<i>S. profundus</i>	>7	>5	7-11	-	17-17	-	-	-
<i>S. saginatus</i>	>5	>7	9-9	10-11	11-16	4-4	8-8	9-9

H). In some individuals, in which all of the series is doubled or tripled (Fig. 35D, E), extra scales appear to be crammed along the dorsal midline rather than spreading laterally and ventrally away from the median series of scales, suggesting that scales lateral to the dorsal ridge series are not appropriated into the median series.

The occasional or complete doubling of the scales in the dorsal ridge scale series is particularly interesting in light of the tendency of macrosemiids (Bartram 1977) and semionotids to develop intercalary scale rows. Flank scale doubling appears to be concentrated in the anterior epaxial region of the fish, and exclusively in the region anterior to the dorsal fin, which is in the same region of the fish as the dorsal ridge scales. It may be significant that the anterior flank is the last region to develop scales in *Lepisosteus* (personal observation), as well as in a variety of paleoniscids (D. Bardack, personal communication).

BODY SHAPE

Newark semionotids exhibit a wide diversity of body form. Such diversity of body form is relatively rare among semionotids from other parts of the world, the one exception being the American Western Triassic (Schaeffer 1967). I recognized 22 different shapes, described either by classification functions from the discriminant analysis, Goodkin viewer tracings, or both. Twenty-two different shapes (including European species) may seem an excessive number, but, in addition to the justifications I have given earlier for defining these groups, the relationship between shape and other characters increases my confidence that the groups are a reasonable first solution to the problem of sorting these fishes by shape.

Particular shapes are not unique within scale groups, but at the same time neither are all shapes duplicated in every scale group. For example, there are deep-bodied fish with both robust scales and modified simple scales, but there are no similar fish with simple or concave scales. Overall, 3 of 22 shapes are duplicated

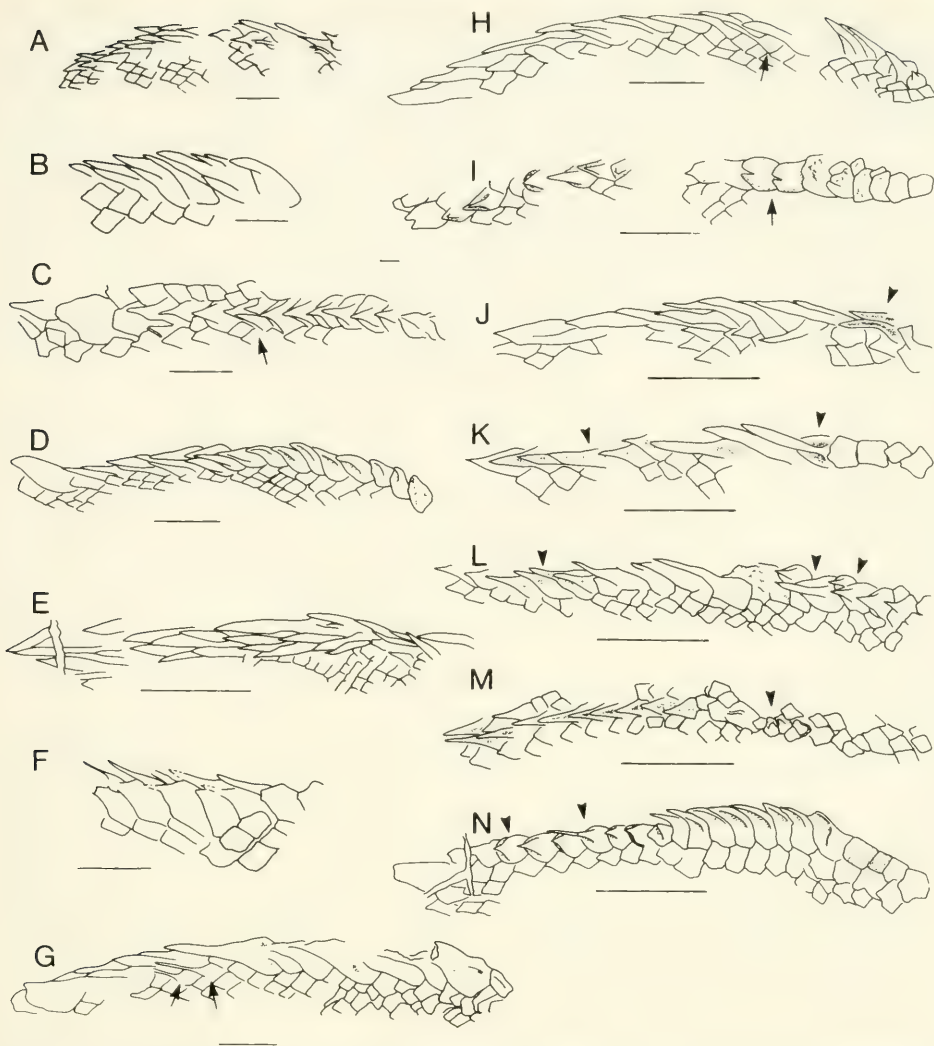


FIG. 35. Dorsal ridge scale anomalies. A, YPM 8865; B, YPM 8758; C, YPM 8861; D, YPM 8847; E, YPM 8848; F, *S. capensis* BMNH P.6861; G, YPM 8719 (note flank scales with "spines"); H, YPM 8812 (note flank scales with "spines"); I, YPM 8845 (split dorsal ridge scales); J, YPM 8750 (note two concave spines anteriorly); K, YPM 8869 (dorsal ridge series is a combination of thin-spined, simple and concave scales); L, YPM 8894 (dorsal ridge series is a combination of thin-spined, simple, and concave scales); M, YPM 8836 (dorsal ridge series is a combination of concave and an uncategorizable convex scale); N, YPM 8932 (dorsal ridge series is a combination of globular, thin-spined and small scales). Scale = 5 mm.

in one or two other scale groups. Species that share the same shape but are distinguished by their dorsal ridge scales are as follows: *S. kirschi* and an undescribed species in the *S. elegans* group (McCune 1982); *S. olseni* and *S. latheticus*; *S. greenwoodi*, *S. virginiae*, and another undescribed species in the *S. elegans* group (McCune 1982). In addition, some groups of species are very similar in shape: *S. decoratus*, *S. thomsoni*, and *S. anosteus*; *S. fundus* and *S. euthenius*. The shapes of all other species are unique.

The relationship between shape and dorsal ridge scale morphology was particularly interesting within the *S. tenuiceps* group. For each of three shape groups in this complex, there was another shape group that was similar though not the same, in my estimation. That each member of these three pairs of similarly shaped

groups should be recognized separately was reinforced by the fact that the two members of each similar pair had different dorsal ridge scales. Three of these six shapes are very similar to, but not quite the same as, the shapes of fishes in other scale groups.

8. RELATIONSHIPS

Beyond initial character selection, schemes of relationship are most heavily determined by assignments of character polarities. Therefore, before discussing the relationships of semionotids, I will explicate my rationale for assigning particular character polarities.

For most meristic characters, the polarity of character states is reasonably straightforward. Serrated scales are found in several actinopterygians, such as *Pteronisculus* (Lehman 1952) and a number of macrosemiids (Bartram 1977), but flank scales with smooth posterior margins are much more widespread among actinopterygians, including *Acentrophorus* (Gill 1923), parasemionotids (Lehman 1952), and a wide variety of paleoniscids. Therefore, I consider serrated flank scales in *S. normanniae* and *S. minor* to be derived.

It is more ambiguous whether the forked caudal fin in *S. virginiae* and *S. thomsoni* is primitive or derived. On the basis of commonality in semionotids, one would conclude that a forked caudal fin is derived. Both forked and weakly emarginate caudal fins are found among macrosemiids (Bartram 1977), but parasemionotids (Lehman 1952), *L. elvensis* (personal observation), and *Acentrophorus* (Gill 1923) have weakly emarginate caudal fins. Because of these last outgroup comparisons, I suggest that a weakly emarginate caudal fin is primitive for *Semionotus*.

The low lateral line scale counts (30–32) in *S. fundus*, *S. kapffi*, and *S. amplicephalus* are derived. Macrosemiids have 34–50 lateral line scales (Bartram 1977). Lepisosteids have 53–62 (Suttkus 1963), and *L. elvensis* has 37–38. In general, the deeper-bodied and slender-bodied forms are probably derived, though specifying a particular form as primitive hardly seems possible.

The probable primitive condition for dorsal ridge scale morphology in semionotids is convex with posteriorly directed spines. Similar dorsal scales are known in paleoniscids and elonichthyids (Orlov 1967), but not generally throughout the actinopterygians. In the paleoniscids and elonichthyids that have dorsal ridge scales, the form of the scales is simple and convex with posteriorly directed spines. Dorsal ridge scales of most *Lepidotes*, all European *Semionotus*, and some American semionotids also have this morphology. *L. mantelli*, *L. toombsi*, *L. laevis*, and nearly all species of *Semionotus* from sediments outside the Newark Supergroup (the exception being some *S. tenuiceps* scales from the lower Lufeng of China (Olsen and others 1982) have simple or modified simple, convex dorsal ridge scales. However, the dorsal ridge scales of many American *Semionotus* are modified in different ways (Olsen and others 1982).

With semionotids it is particularly difficult to determine the polarities for the two most important character complexes, dorsal ridge scale morphology and body shape. The problem stems from the fact that both characters have many more than two states—22 in the case of shape and 7 in the case of dorsal ridge scales—and also from operational difficulties relating to coding the characters (or character complexes).

In the case of body shape, it is possible to code the single character “body shape” as the ranges of the ratios of two measurements, such as depth/standard length or head length/standard length. Aside from the obvious difficulty of defining discrete character states from continuous variables, the high correlation of these body measurements would severely bias the outcome toward a solution based entirely on shape. Another possibility would be to recognize formally the generalization that both extremes of shape (generally slender or deep) are derived relative to the fishes of middle body depths, but it is misleading to label two deep-

bodied but differently shaped fish as sharing uniquely derived character states. The most desirable solution would be to understand the transformation from one shape to another developmentally or to describe it mathematically. The former is impossible with fossils, and the latter analysis is beyond the scope of the present work, but a solution along the lines discussed by Bookstein (1978), Humphries and others (1981), or Raup (1966) is certainly possible (cf. Bookstein and others 1985, published after this study was completed). However, a sufficient mathematical description would not necessarily describe the true developmental (Raff and Kauffman 1982) or evolutionary transformation.

In the absence of a mathematical or developmental rationale for the polarity of shape transformation in these fishes, I have chosen to consider the many states of the character "shape" as equally derived. At present, this is the least misleading null hypothesis. A future analysis may resolve this difficulty.

The criterion for recognizing a shared shape was the same as for incorporating an individual fish into a Goodkin viewer group (see Chapter 4). This convention leaves only the loose end of determining which of the 22 shapes is primitive. However, if no transformational scenario about shape is advanced, the taxonomic value of shape is limited to describing species; for that function, both primitive and derived shapes are equally useful.

Devising a transformation series of the different dorsal ridge scale series appears more tractable than it was for body shape. There are fewer patterns of dorsal ridge scales, more easily ordered, than there are shapes. Even so, the correct way to code the dorsal ridge scale series is not obvious. Does one type of dorsal ridge scale series constitute a single character state, or should the dorsal ridge scale series be treated as a complex of characters and coded as several characters? If the dorsal ridge scale series were treated as a single character, then there would be two relatively simple hypotheses of character transformation. If different scale types were independently derived, then the resulting single character cladogram would be a hexachotomy (Fig. 36A). Alternatively, the dorsal ridge scales can be ordered in a relatively straightforward morphological series (Fig. 36B), resulting in a better-resolved (but not necessarily more correct) one-character cladogram (Fig. 36C).

A third alternative is to atomize the morphology of the dorsal ridge scale series into five two-state characters (Fig. 37). The many-character cladogram (Fig. 38) was constructed using this system of coding for the dorsal ridge scale complex. Aspects of dorsal ridge scale morphology dominate the structure of the cladogram because body shape, and a large portion of other characters, serve only to define species, not to relate them to each other. Species having identical shapes but different dorsal ridge scales are grouped by the latter, and shared shapes are represented as homoplastic (shapes 15, 16, and 17 in Fig. 38). All other shapes are shown as autapomorphies defining species.

It is possible, given the patterns of variation discussed earlier, that considerable homoplasy has remained undetected in dorsal ridge scale characters. The occurrences of supernumerary spines and dorsal ridge scale "sports" misplaced in series of differing morphologies suggest that all or many semionotid species have the genetic/developmental potential necessary to generate any of the dorsal ridge scale patterns actually observed (in the sense of atavisms; see Hall 1984), though the expression of this potential may usually be hidden.

One of the most striking features of the cladogram is the number of unresolved polychotomies. Of the eight nodes defined by one or more synapomorphies, five of these are polychotomies—nodes that include between three and nine branches. Although there is nothing intrinsically wrong with polychotomies, they are often

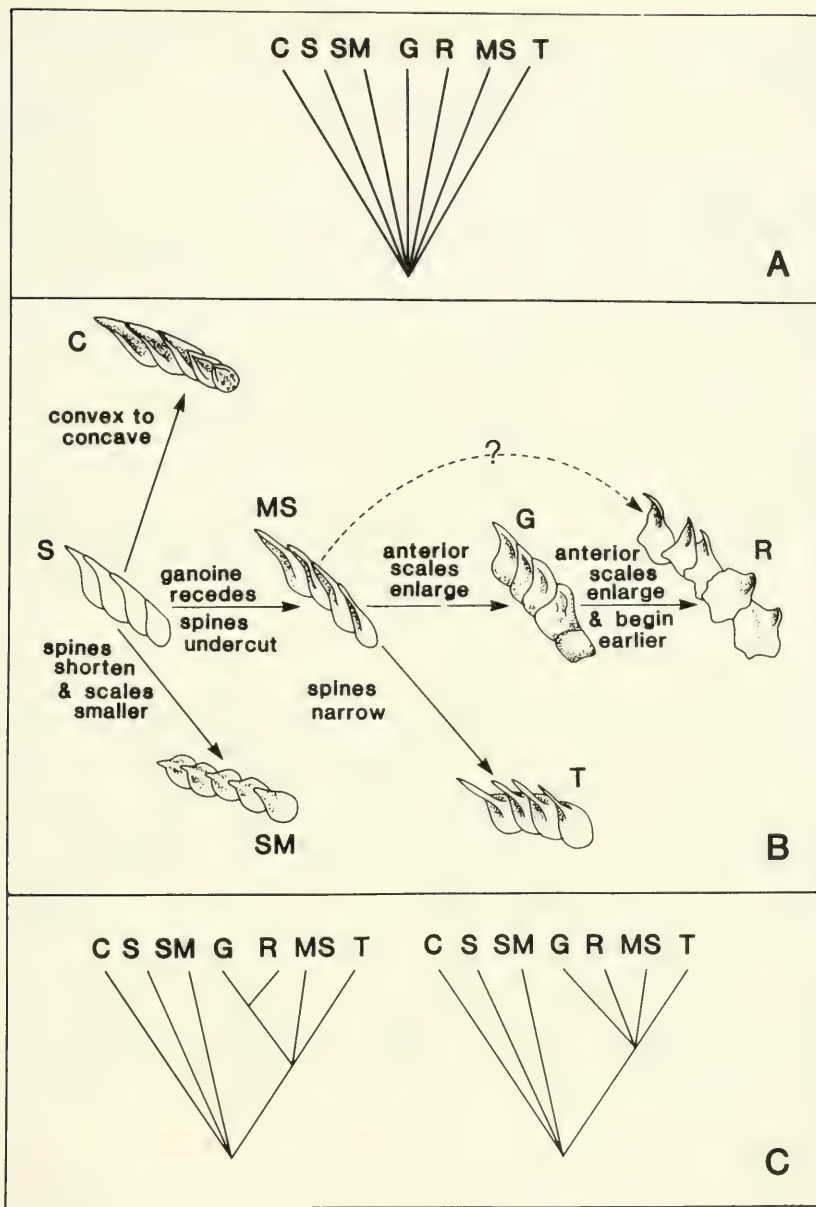


FIG. 36. Hypotheses of character transformations. S = simple scales, MS = modified simple, G = globular, R = robust, C = concave, SM = small scale, T = thin-spined. A, A hexachotomy, the simplest hypothesis of transformation for the seven types of dorsal ridge scales in semionotids from P4.

B, Hypothesized morphological transformation for dorsal ridge scales in semionotids from P4. The dotted line indicates ambiguity as to whether "R" scales were derived from "G" scales or directly from "MS" scales.

The transformation of simple to modified simple scales involves a decrease in the area of the dorsal surface covered by ganoine and slight undercutting lateral to the spine. Extreme reduction of the bone under the scale spine yields thin-spined from modified simple. Increase in the mass of the anterior scales (except the four most anterior ones) of modified simple and continued recession of ganoine would result in globular scales. Robust scales might derive from either an anterior shift in the position of enlarged scales and a general increase in size from globular scales or from an independent size increase of anterior scales (starting with more anterior scales than in the globular type) from modified simple scales. Small scales could be derived by shortening of the spine from simple scales.

C, Two alternative character branching sequences based on hypothesized morphological transformation in B. The difference between these alternatives is the derivation of "R" scales from either "G" or "MS" scales.

CHARACTER	CHARACTER STATES	SCALE TYPE						
		S	C	MS	G	R	SM	T
shape	convex/concave	0	1	0	0	0	0	0
lateral undercutting	no/yes	0	0	1	1	1	0	1
size anterior scales	small/large	0	0	0	1	2	0	0
spine length	long/short	0	0	0	0	0	1	0
scale size	normal/small	0	0	0	0	0	1	0
ganoine cover	complete/partial	0	0	1	1	1	0	1
spine width	normal/narrow	0	0	0	1	0	0	0

FIG. 37. System to recode the seven-state dorsal ridge scale character into seven two-state (or three-state) characters. Abbreviations are the same as those given for Fig. 36. Under character state, the primitive state (0) is listed first, the derived states (1, 2) second and third, respectively. Simple scales are taken to be primitive for all seven new characters.

thought to arise from “partial ignorance” (Nelson 1980), owing to shortages of specimens, taxa, or characters, particularly in paleontological studies (Patterson and Rosen 1977). However, in Newark semionotids, the kinds of characters as well as the general completeness and high quality of specimens require us to accept the present character distributions until contrary evidence accrues. A large proportion of living species of fishes (within a particular family) can be recognized on the basis of the sorts of characters I have used for semionotids—scale counts, scale morphology, fin ray counts, teeth, fin characters, and body proportions. Color, behavior, and ecology are notably absent from fossils, but they are also absent in the museum specimens of extant species that have accumulated over many decades and on which much of fish taxonomy has been based. Furthermore, as discussed by McCune and others (1984), in cladograms of species, especially diverse groups, polychotomies can represent true character distributions and not simply incomplete analyses.

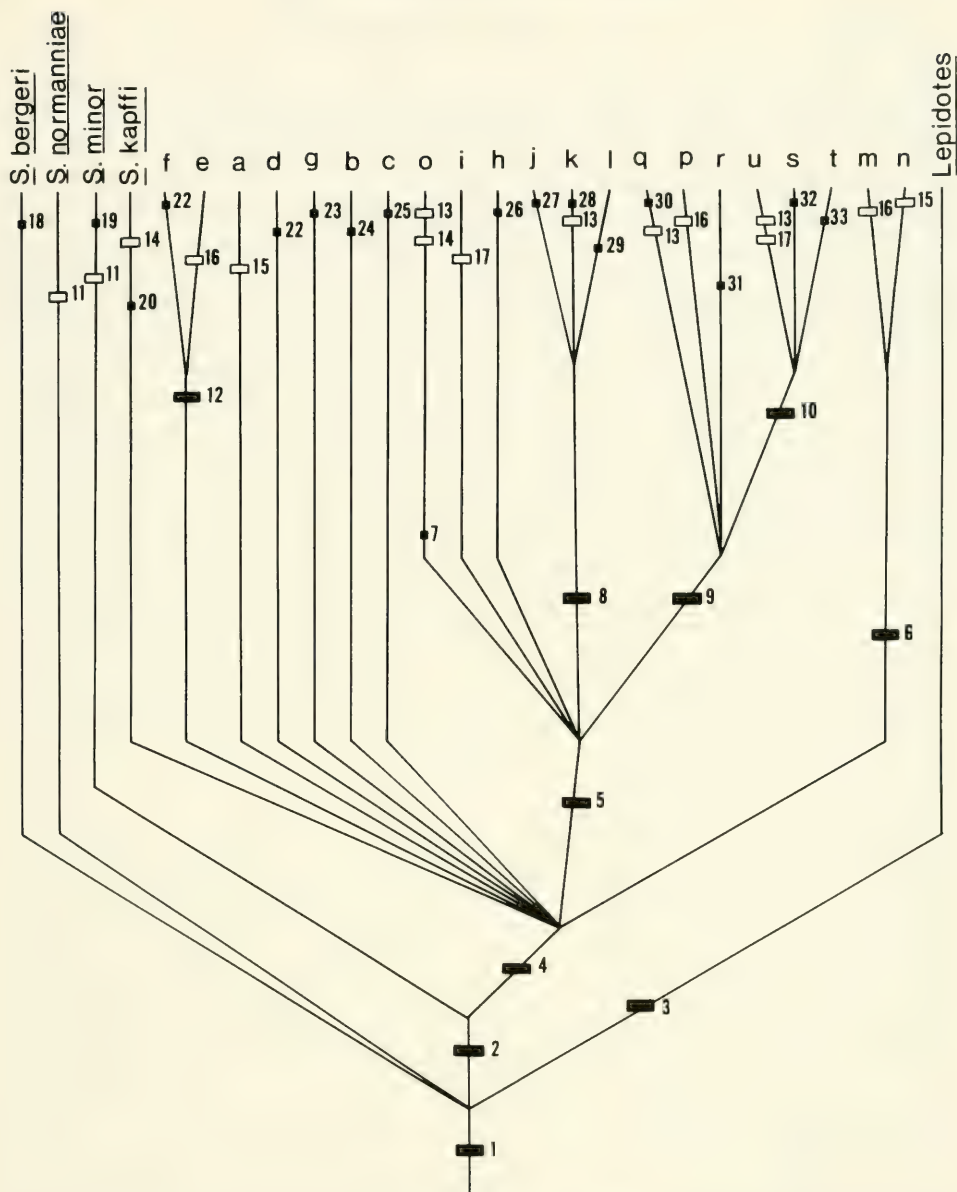


FIG. 38. Tentative cladistic relationships for semionotids from P4 (descriptions for some species unpublished; see McCune 1982) and European semionotids (McCune 1986). Species a through u (also pictured in Fig. 39) are as follows: a = *S. kirschi*, b = *S. redfieldii*, c = *S. euthenius*, d = *S. olseni*, e = *S. virginiae*, f = *S. thomsoni*, g = *S. convalis*, h = *S. anosteus*, i = *S. schaefferi*, j = *S. johberryi*, k = *S. latheticus*, l = *S. melaninus*, m = undescribed species in *S. elegans* group, n = undescribed species in *S. elegans* group, o = *S. amplicephalus*, p = *S. greenwoodi*, q = *S. fundus*, r = *S. saginatus*, s = *S. decoratus*, t = *S. tenuiceps*, and u = *S. profundus*. Large black bars are synapomorphies. Small black bars are autapomorphies. White represents homoplasies. Primitive character states are not shown. Key to derived character states is as follows: 1, Dorsal ridge scales present, premaxillae with long rostral process, epiotic with posteriorly directed process, lachrymal serially subdivided. 2, Fringing fulcra reduced in number. 3, Suborbitals number greater than one. 4, Basal fin fulcra reduced in number. 5, Dorsal ridge scales laterally undercut. 6, Dorsal ridge scales concave. 7, Dorsal ridge scales with short spines, dorsal ridge scales small relative to flank scales. 8, Dorsal ridge scale spines very narrow and separated distally from base. 9, Anterior dorsal ridge scales enlarged. 10, Anterior dorsal ridge scales even larger. 11, Flank scales serrated. 12, Caudal fin forked. 13, Horizontal flank scale rows reduced in number. 14, Vertical flank scale rows reduced in number. 15, Shape "1." 16, Shape "2." 17, Shape "3." 18–33, Autapomorphic shapes. Reproduced from McCune and others, 1984, Semionotid fishes from the Mesozoic great lakes of North America, p. 27–44. In A. A. Echelle and I. Kornfeld [eds.] Evolution of fish species flocks. University of Maine Press, Orono.

9. CONCLUDING REMARKS

Lake cycle P4 exhibits a diversity of species within a single family heretofore unknown in fossil fishes. There are 21 species of semionotid fishes that once dominated this single lake (Fig. 39), and the diversity of P4 semionotids is only one small portion of the total semionotid diversity in eastern North America (most of it undescribed). Most aspects of the morphology of *Semionotus* from P4 are not different among species. In the fauna as a whole, only two fields of morphology—dorsal ridge scales and body shape—are significantly variable. Diversity of body shape is quite common in fishes (McCune 1981, and references therein), but even so the range of body shape within the North American representatives of *Semionotus* is far greater than the variation in most genera of living fishes. Variation in dorsal ridge scale morphology is known in semionotids and to a limited extent in a few other fossil groups (see Orlov 1967). Although the functional significance of dorsal ridge scales is not yet understood, the pattern of anomalous variation in relation to consistent patterns of variation of dorsal ridge scales may have general significance for systematics and evolution.

That many semionotids and their sister-group macrosemiids do funny things with their scales in the anterior epaxial region suggests that the developmental system controlling these scales is particularly labile or uncanalized. This is a restatement of the fact that the morphology of dorsal ridge scales is variable in semionotids; something like it could be said about the bills of honeycreepers and finches or the teeth of cichlids. From the fact that thin-spined or small scales may

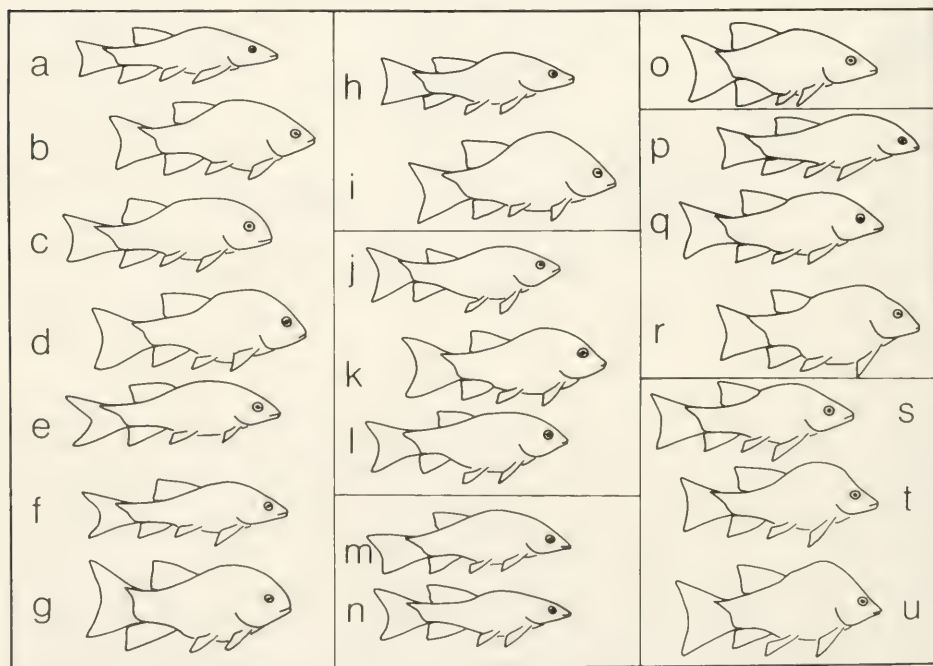


FIG. 39. The semionotid assemblage from P4. Species are grouped by their dorsal ridge scales. Species with simple scales are a = *S. kirschi*, b = *S. redfieldii*, c = *S. euthenius*, d = *S. olseni*, e = *S. virginiae*, f = *S. thomsoni*, g = *S. convalis*. Species with modified-simple scales are h = *S. anosteus*, i = *S. schaefferi*. Species with thin-spined scales are j = *S. johberryi*, k = *S. latheticus*, l = *S. melaninus*. Species with concave scales are m = undescribed species in *S. elegans* group, n = undescribed species in *S. elegans* group. Species with globular scales are p = *S. greenwoodi*, q = *S. fundus*, r = *S. saginatus*. Species with robust scales are s = *S. decoratus*, t = *S. tenuiceps*, u = *S. profundus*.

appear (rarely) in a globular series, I begin to suspect that many semionotids may have more or less the same hidden potential (in the sense of atavisms; see Hall 1984) to produce most scale types. For systematics, this hidden potential may imply a high probability of widespread parallelism and a low confidence in the most parsimonious cladogram. The implication from the pattern of variability of dorsal ridge scales for evolution as a process is that evolution is not simply a linear accumulation of phenotypic/genotypic acquisitions. If genetic-developmental potentials are shared (primitively) by large groups (see Roth 1984), the generation of diversity, especially in speciose groups, may come less from the accumulation of mutations in reproductively isolated populations than from the selective unmasking and mixing of already present and cryptically accumulating (see Rachootin and Thomson 1981) genetic potentials.

Although the manipulative experiments that one might want to conduct to understand the generation of variability in dorsal ridge scales or body shape are clearly impossible, a long series of historical experiments has proceeded over and over again through time, and simultaneously in a number of geographically distinct lake basins. We need only to collect and analyze data and interpret the results. In this work I have begun to develop a species-level taxonomy that I hope will be a useful vocabulary for asking questions about the paleoecology and evolution of semionotid fishes in Newark lakes.

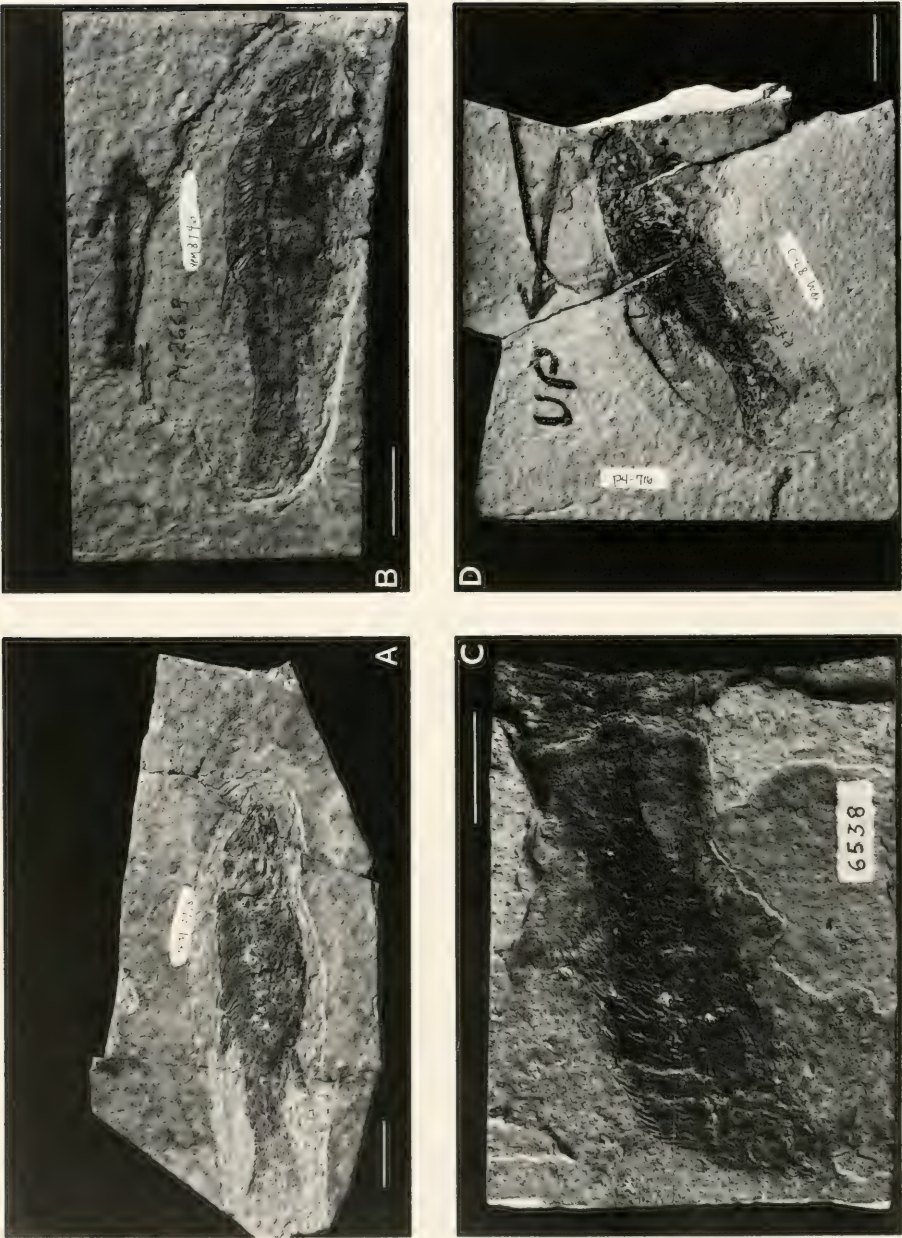


FIG. 40. Holotypes of four new species. A, *S. kirschi* YPM 8718; B, *S. thomsoni* YPM 8746; C, *S. olseni* YPM 6538; D, *S. virginiae* YPM 8740. Scale = 2 cm.

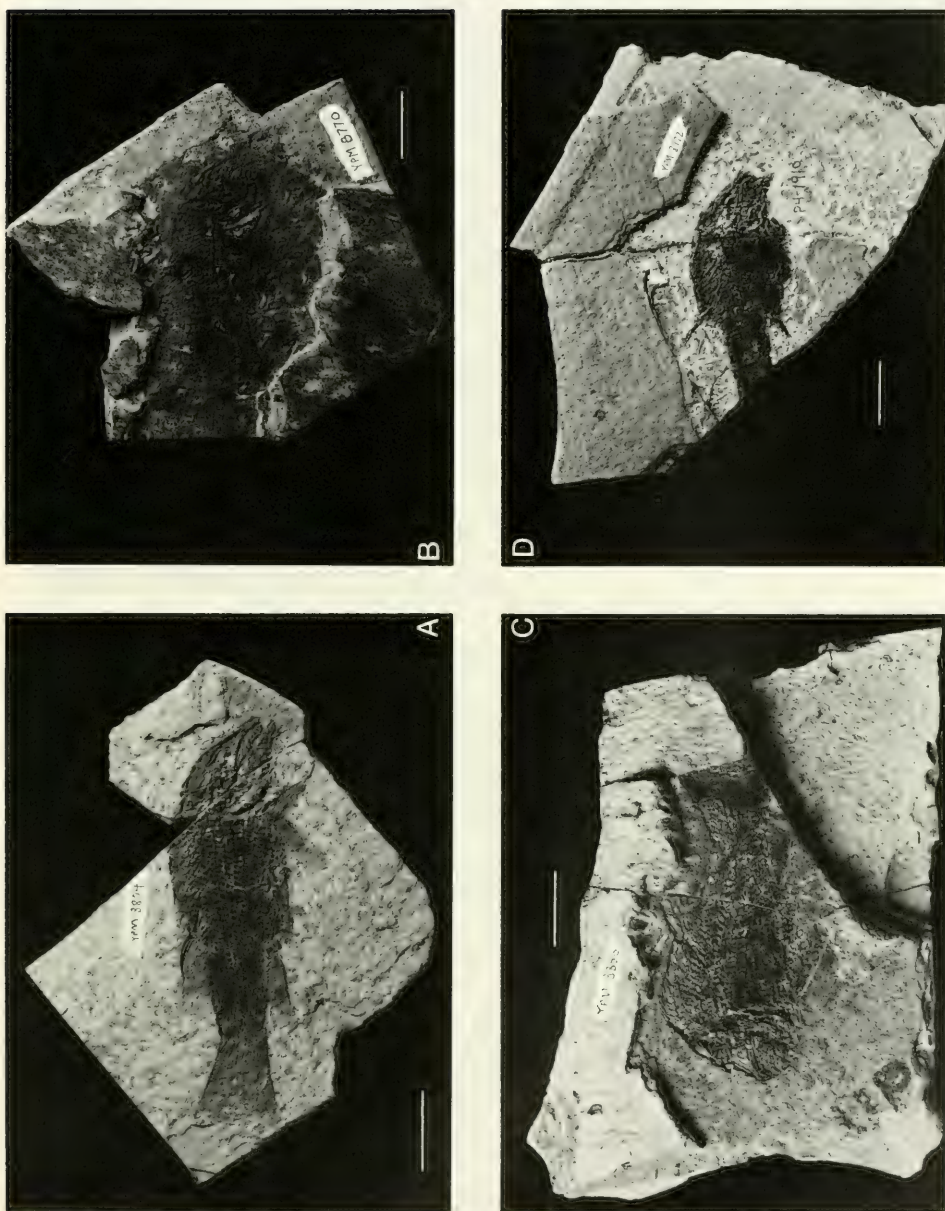


FIG. 41. Holotypes of four new species. A, *S. euthenius* YPM 8804; B, *S. convalis* YPM 8770; C, *S. schaefferi* YPM 8856; D, *S. redfieldii* YPM 8772. Scale = 2 cm.





FIG. 42. Holotypes of five new species. A, *S. johberryi* YPM 8800; B, *S. anosteus* YPM 8844; C, *S. latheticus* YPM 8899; D, *S. melaninus* YPM 8840; E, *S. amplicephalus* YPM 8849. Scale = 2 cm.

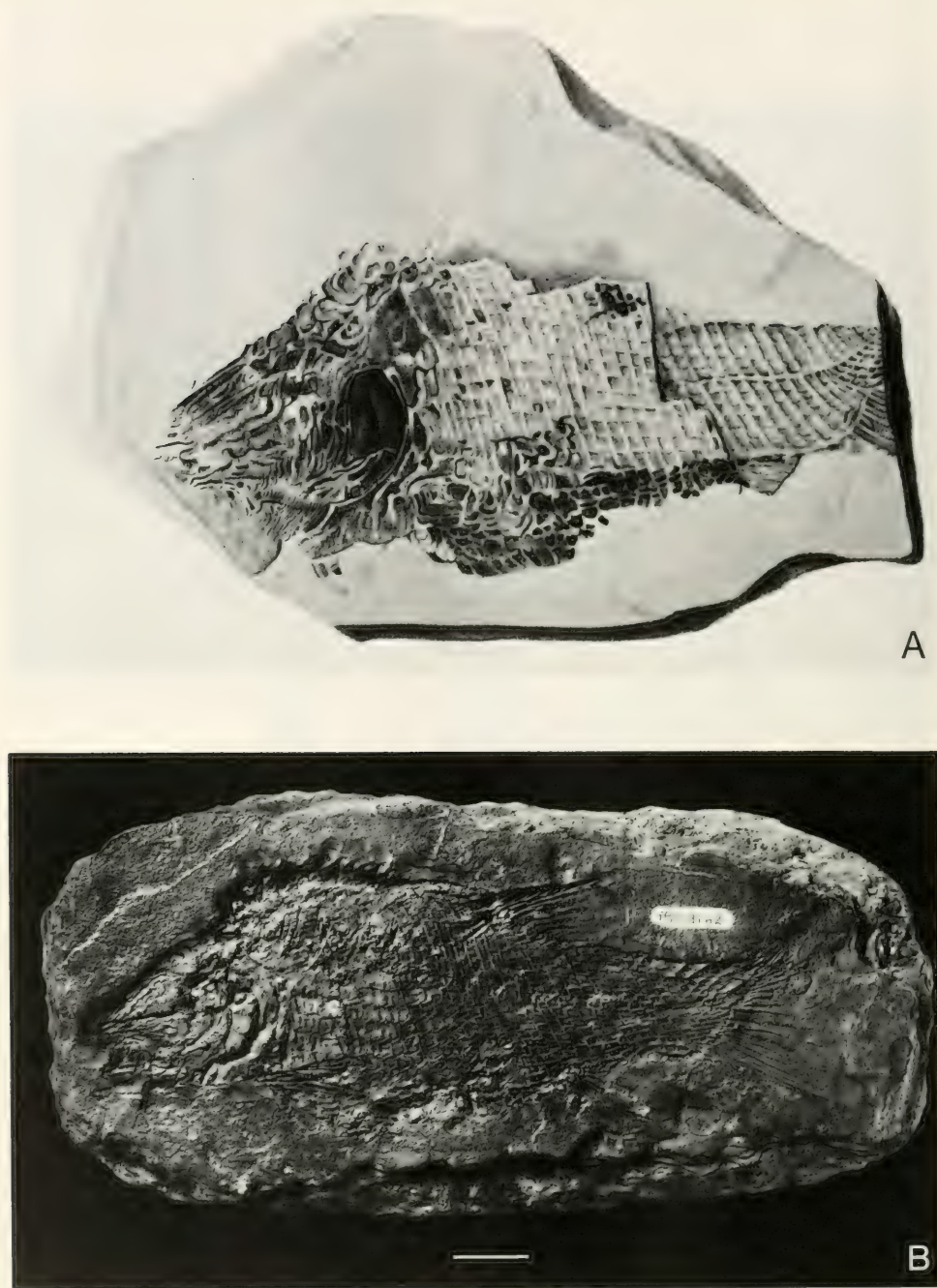


FIG. 43. *S. tenuiceps*. A, original of *S. tenuiceps* (Agassiz) = "*Eurynotes tenuiceps*" Agassiz. From Agassiz (1836) pl. 4, fig. 4. B, neotype of *S. tenuiceps* YPM 8162, from Sunderland, Massachusetts. Specimen was negatively prepared. Scale = 2 cm.

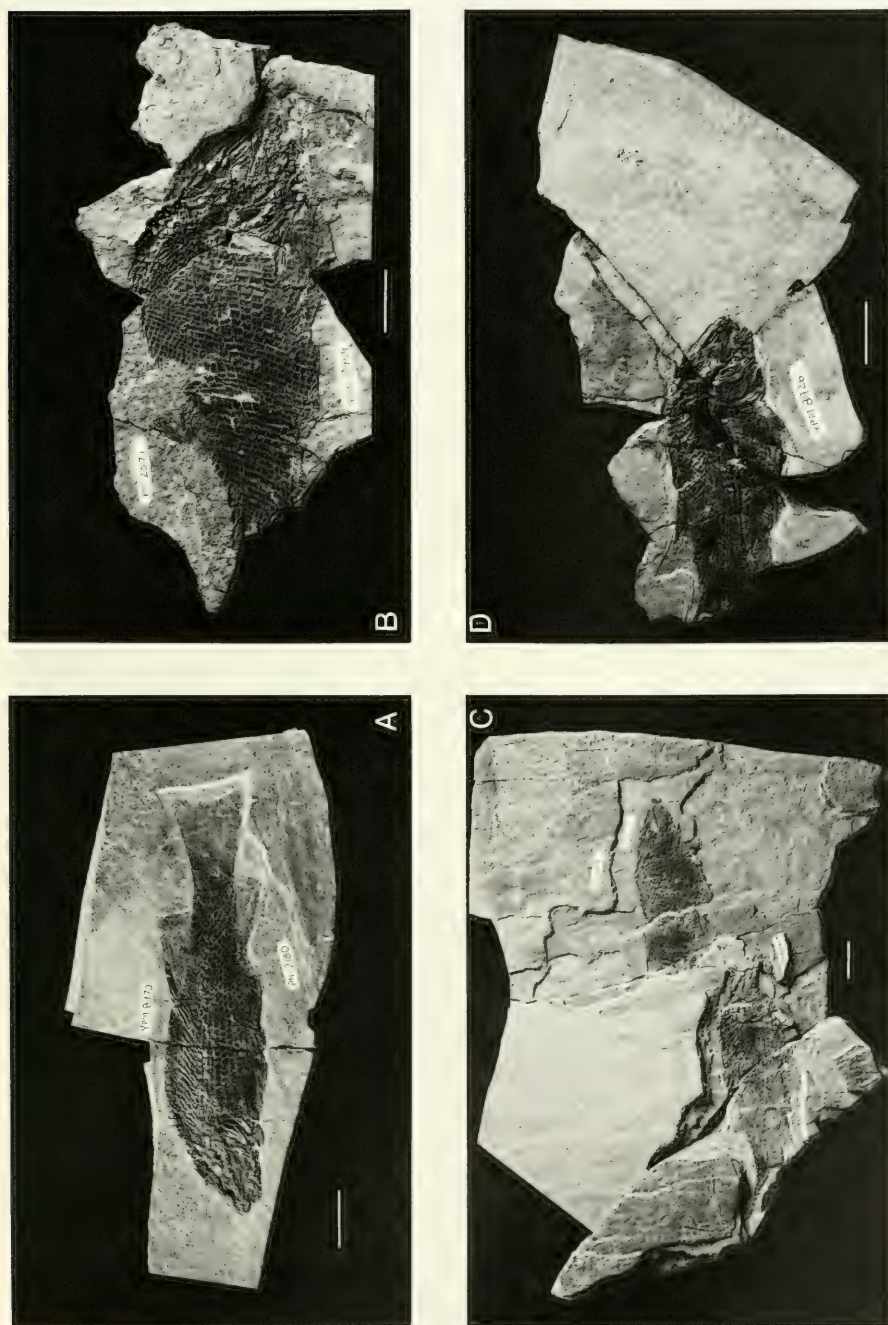


FIG. 44. Holotypes of four new species, A, *S. greenwoodi* YPM 8970; B, *S. profundus* YPM 8944; C, *S. decoratus* YPM 8958; D, *S. fundus* YPM 8926. Scale = 2 cm.



FIG. 45. Holotype of *S. saginatus* YPM 8932. Scale = 2 cm.

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